TAPHONOMY AND PALAEOECOLOGY OF AN ASSEMBLAGE OF LARGE MAMMALS: HYAENID ACTIVITY IN THE LOWER PLEISTOCENE SITE AT VENTA MICENA (ORCE, GUADIX-BAZA BASIN, GRANADA, SPAIN)

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ABSTRACT - We report taphonomic and palaeoecologic data on the rich, diverse and well preserved assemblage of large mammals from Lower Pleistocene deposits at Venta Micena (Orce, Granada, south-east Spain). The biostratigraphic and diagenetic characteristics of the assemblage are congruous with the sedimentary context deduced from the study of the site, and both confirm that: (i) the assemblage represents an accumulated taphonomic stage, (ii) it was formed by demic, autochthonous palaeobiologic entities, which were preserved and recorded in situ, and (iii) it is the result of biological processes and agents. Interspecific analysis of size/abundance patterns in ungulates shows that the main taphonomic bias affecting the bones was produced by biological destruction before burial, and that the loss of information was greater for species of smaller body size. Factor correspondence analysis was used to compare the frequencies at which some groups of postcranial elements are represented in several recent and archaeological bone assemblages accumulated by carnivores, rodents and hominids. The results obtained strongly suggest that the bones from Venta Micena were collected mainly by hyaenids, which deposited them near shallow dens excavated around the ponds that surrounded the Pleistocene lake of Orce. An analysis of the abundance of major long bones has shown that differential fragmentation was produced by hyaenids as a function of their structural density and mean marrow content. All these data allow to formulate a descriptive-quantitative model for the characterization of bone assemblages generated from hyaenid activity, in which Venta Micena is an example of bone concentration and modification activities by *Pachycrocuta brevirostris*. Strong selection of prey by carnivores (which killed preferably juveniles, females and individuals with diminished locomotive capabilities among ungulate prey species of larger body size) is indicated by (i) the abundance of juvenile individuals with deciduous teeth in relation to the average weight estimated for adults in each ungulate species, by (ii) the U-shaped atritional mortality profiles deduced from crown height measurements, by (iii) the presence of many metapodial with different osteopathologies, and by (iv) a biased sexual ratio deduced from the metacarpals of large bovids. Comparison between the frequencies in which modern African carnivores kill and scavenge ungulates from different size classes and the abundance of these size categories in the assemblage suggests that the Venta Micena hyaena was a bone-cracking scavenger which fed largely on carcasses of ungulates preyed upon and partially consumed by flesh-eating carnivores such as saber-toothed felines and wild dogs.

KEYWORDS: BONE ASSEMBLAGE, TAPHONOMY, PALAEOECOLOGY, MULTIVARIATE ANALYSIS, LOWER PLEISTOCENE, SPAIN.

RÉSUMÉ - Ce travail est l'étude taphonomique et paléoécologique d'un assemblage abondant et diversifié de grands mammifères provenant du gisement de Venta Micena (Pléistocène inférieur, Orce, Grenade, Sud-Est de l'Espagne). Les caractéristiques biostratigraphiques et diagénétiques de l'assemblage s'accordent avec le contexte sédimentaire déduit de l'étude du gisement, les deux approches confirmant (1) que l'assemblage représente un ensemble taphonomique d'accumulation, (2) qu'il fut formé par des entités paléobiologiques autochtones et dèmesiques, préservées et enregistrées in situ et (3) qu'il est le résultat d'agents et de processus biologiques. L'examen interspécifique des données, taille/abondance des espèces d'ongulés, montre que les principaux biais taphonomiques sont dus à une destruction biologique avant l'ensevelissement et concernent principalement les espèces de petite taille. L'analyse factorielle des correspondances est utilisée pour comparer les fréquences des différents groupes d'éléments du squelette post-crânien rencontrés dans des ensembles récents ou archéologiques d'ossemens accumulés par les carnivores, les rongeurs et les hommes. Les résultats obtenus suggèrent que les restes de Venta Micena ont été récoltés principalement par des hyènes qui les ont déposés autour de l'entrée de leurs repaires peu profonds, creusés près
des mares qui bordaient le lac pléistocène d’Orce. L’étude de l’abondance des principaux os longs conservés dans l’assemblage montre que les hyènes réalisaient une fragmentation différentielle des os en fonction de leur densité minérale et de leur contenu moyen en moëlle osseuse. Avec ces données, nous pouvons présenter un modèle descriptif-quantitatif pour la caractérisation des assemblages osseux résultant de l’activité des hyènes dont Venta Micena est un exemple de concentration et de modification résultant de l’action de *Pachycrocuta brevirostris*. L’importante sélection des proies par des carnivores qui chassaient principalement des individus jeunes, des femelles et des sujets à capacité locomotrice réduite dans le cas d’ongulés de grande taille, est démontrée par (1) l’abondance des individus jeunes (présence de la dentition déciduale) et la relation avec le poids estimé pour les adultes de chaque espèce; (2) par la courbe de mortalité en U obtenue à partir des mesures de hauteur de la couronne dentaire; (3) de la présence de nombreux métapodes avec diverses ostéopathologies; (4) de la proportion des sexes déduite de la morphométrie des métacarpiens des grands bovidés. Finalement, la comparaison entre la fréquence observée chez les carnivores africains actuels chasseurs et charognards d’ongulés de diverses classes de taille et l’abondance de ces catégories de taille dans l’assemblage fossilis suggère que la hyène de Venta Micena avait un comportement de charognard, s’appropriant les cadavres consommés pour partie par les autres carnivores, tels les félinés à dents de sabre et les chiens sauvages.

**MOTS-CLÉS:** ASSEMBLAGE OSSEUX, TAPHONOMIE, PALÉOÉCOLOGIE, ANALYSE MULTIVARIÉE, PLÉISTOCÈNE INFÉRIEUR, VENTA MICENA.

**RESUMEN** - En este trabajo se efectúa un estudio tafonómico y paleoecológico de la abundante y diversa asociación de grandes mamíferos proveniente del yacimiento de Venta Micena (Pleistoceno inferior; Orce, Granada, sureste de España). Las características bioestratigráficas y diagenéticas de la asociación fósil son congruentes con el contexto sedimentario deducido del estudio del yacimiento, confirmando ambas que: (i) la asociación presenta un estado tafonómico de acumulado, (ii) se encuentra formada por entidades paleobiológicas dèmeicas, por entidades conservadas autótonas y por entidades registradas in situ, y (iii) es el resultado de la acción de procesos y agentes biológicos. El análisis interspecífico de los patrones de tamaño/abundancia en las especies de unglados ha puesto de manifiesto que los principales sesgos tafonómicos se produjeron como consecuencia de la destrucción por agentes biológicos de los restos óseos en la etapa previa a su enterramiento, afectando la pérdida de información más a las especies con dimensiones corporales reducidas. El análisis factorial de correspondencias se usó para comparar las frecuencias en que distintos grupos de elementos esqueléticos postcraneales se encuentran representados en asociaciones recientes y arqueológicas de huesos acumulados por carnívoros, roedores y homínidos. Los resultados obtenidos sugieren que los restos de Venta Micena fueron recolectados principalmente por las hienas, quienes los depositaron en torno a la entrada de cubiles poco profundos, excavados cerca de las charcas que bordeaban el lago pleistoceno de Orce. Un análisis de la abundancia de los principales huesos largos preservados en la asociación ha mostrado que las hienas produjeron una fragmentación diferencial de acuerdo con su densidad mineral y su contenido medio en médula ósea. Todo ello permite presentar un modelo descriptivo-quantitativo para la caracterización de asociaciones óseas generadas por la actividad de los hienidos, pudiendo ser Venta Micena el ejemplo de actividad concentradora-modificadora de los representantes de la especie *Pachycrocuta brevirostris*. Se ha podido deducir una intensa selección de presas por parte de los carnívoros, los cuales cazaban preferentemente individuos jóvenes, hembras y ejemplares con capacidad locomotriz disminuida en el caso de las especies de unglados con mayor tamaño. Las evidencias que apoyan este modelo son: (i) la abundancia de individuos jóvenes, con dentición decidua, en relación al peso estimado para los adultos de cada especie; (ii) las presencias de meteorización gradual con forma de U, inferibles de las medidas de altura de la corona dentaria; (iii) la presencia de abundantes metapodos que muestran diversas ostéopatologías; y (iv) la proporción de sexos deducible a partir de los metacarpianos de los grandes bóvidos. Finalmente, la comparación entre la frecuencia en que los carnívoros modernos africanos cazan y carroñean unglados de diferentes clases de tamaño y la abundancia de estas categorías en la asociación fósil sugiere que la hiena de Venta Micena era básicamente carroñera, aprovechando los cadáveres de presas cazadas y consumidas por parte por otros carnívoros comedores de carne y no fracturadores de huesos, tales como los félinos con dientes en forma de sable y los perros salvajes.

**PALABRAS CLAVE:** ASOCIACIÓN ÓSEA, TAFONOMÍA, PALEOEKOLOGÍA, ANÁLISIS MULTIVARIANTE, PLEISTOCENO INFERIOR, VENTA MICENA.

**INTRODUCTION AND BACKGROUND**

The Venta Micena site (Orce, Granada, south-east Spain) is located in the eastern sector of the Guadix-Baza basin (Fig. 1). This basin was endorheic until upper Pleistocene times, thus facilitating an exceptional record of the Plio-Quaternary taphocoenoses of large mammals, which were preserved in swamy and lacustrine sediments. Previous studies indicate that the Venta Micena assemblage is included in 90-98% pure micritic limestone, which precipitated in freshwater ponds emplaced on a caliche paleosol of diagenetic origin. This paleosol surrounded a more or less stable and shallow lake with swampy marginal zones that existed in the valley of Orce during the
Plio-Pleistocene (Vera et al. 1985; Soria et al. 1987). Biostratigraphic analyses of the faunal assemblage (Martínez-Navarro 1991, 1992a; Martínez-Navarro & Palmqvist 1995; Turq et al. 1996; Martínez-Navarro et al. 1997) place this site in the lower Pleistocene, with an estimated age of $1.2 \pm 0.2\text{ Ma}$.

The 80-120 cm thick Venta Micena stratum is one of the various fossiliferous units with macromammals in the Plio-Pleistocene sedimentary sequence of Orce, whose surface can be followed along 2.5 km approximately, and stands out topographically in the ravines of the region. All the fertile strata from the Orce-Venta Micena sector are found within a carbonate sequence with mean thickness of 15 m, horizontal stratification undisturbed by tectonic activity, without breaks or discordances, and with a cartographic extension of approximately 16 km$^2$. This sequence shows the following vertical sedimentary evolution: white clayey marly facies with carbonate concretions of diageneric origin and freshwater invertebrates (swamp in central facies); clayey muddy facies with mud-cracks, abundant coal and bony mammal remains (swamp in marginal facies); white carbonate facies (mudstone) with paleosols, carbonate concretions and abundant skeletal remains of fossil mammals (lake with various periods of partial desiccation, during one of which the Venta Micena assemblage was formed).
The fossils from Venta Micena are placed on a paleosol which was developed on sediments deposited during a first lacustrine stage, thus evidencing a generalized descent of the water table in the lake, which was characterized by wide emerged zones (mudcracks and rootmarks) with small shallow ponds (< 1 m depth, 2-20 m diameter) (Gibert et al. 1992). The assemblage is embedded in homogeneous and porous micritic sediments, which precipitated during a period of partial expansion of the ponds (restricted swampy biotope of carbonate facies, with plants colonizing the border of the ponds), and it was closed over by a massive precipitation of micrite produced during an immediately subsequent phase of uprising of the water table in the lake (lacustrine stage two). This welling was rather slow, as suggests the absence of terrigenous, erosive structures, and of any evidence of sediment traction. The micrite which precipitated during both lacustrine stages is very similar, both texturally and structurally.

The accumulation of skeletal remains in Venta Micena (Gibert & Caporici 1989; Gibert et al. 1992; Palmqvist et al. 1992, 1993) was exclusively due to the biotic factors. Geologic processes, such as fluvial transport, can be excluded, since the bones are randomly oriented, and show no traces of abrasion from rolling or similar movements. Furthermore, many bones were for some time exposed to the elements, and a very high percentage of specimens show clear marks of carnivore damage (with almost total dismembering of all elements, and bite marks and breakage in the most vulnerable places).

The palaeoecological analyses of this fossil community (Martínez-Navarro 1991, 1992b; Mendoza et al. 1993) have been based both on isogram methodology (Valverde 1967; Legendre 1986) and on multivariate comparisons with several types of modern mammalian communities (Reed 1997). The results obtained suggest that the composition of the palaeocommunity of Venta Micena, in terms of the relative abundance of groups of species established according to their size and with the type of trophic resources used, was similar to that of present day communities of large mammals inhabiting African savannas with tall grass and spiny trees.


The presence of humans in the southern Iberian Peninsula during lower Pleistocene times is supported by the finding of a few fossil remains which were tentatively attributed to Homo sp. (a polemic cranial fragment which has generated considerable debate and a humeral diaphysis from Venta Micena; Gibert et al. 1994; Gibert & Palmqvist 1995; Zihlman & Lowenstein 1996; Palmqvist 1997; a medial phalanx from the karstic site at Cueva Victoria; Palmqvist et al. 1996b), and by undoubted stone artefacts found in situ in the lower Pleistocene site at Fuente Nueva-3a (1.07 Ma), which show a very simple technology not essentially different from the Oldowan and Developed Oldowan types found in sub-Saharan Africa (Tixier et al. 1995; Turq et al. 1996; Martinez-Navarro et al. 1997). It is interesting to point out that the human mandible and lithic industries found in the lower Pleistocene (> 1.6 Ma) deposits from Dmanis, East Georgia (Gabunia & Vekua 1995) are associated with M. whitei, the African machairodont also present in Venta Micena (Martinez-Navarro & Palmqvist 1995, 1996), which indicates extensive faunal dispersal from Africa to Eurasia in the lower Pleistocene.

The objectives of this study are: (i) to determine whether the faunal assemblage preserved the structure of the original palaeosociocones; (ii) to identify more accurately the biological agents responsible for the modification and accumulation of the assemblage; and (iii) to study the interspecific relationships that existed in the palaeocommunity, such as those produced by the predatory activity of carnivores.

THE VENTA MICENA STRATUM

The Venta Micena stratum has a mean thickness of 1 m and presents the following vertical structure from bottom to top (Fig. 2):

- A basal level (lacustrine stage 1) whose thickness is between one third and half of the stratum, formed by homogeneous micritic sediments with
some carbonate nodules (5-20 cm thick), small mud banks and microscopic fossil shells of freshwater mollusks (among them, *Melanoideis tuberculata*, an eurythermal species which colonizes a wide range of biotopes according to Anadón et al. 1987).

- A 4-15 mm thick calcere paleosol (hardpan), which forms an irregular surface, subparallel to the bedding plane, and is thicker at the highest topographic heights.

- A new level of homogeneous and porous micrite sediments (lacustrine stage 2), which continues up to the top of the stratum, showing numerous rootmarks and mudcracks, which are more abundant in its lower part, and a high density of fossil bones of large mammals; this very restricted vertical interval in the distribution of fossils, marks the palaeontological site at Venta Micena.

The macroscopic, petrographic, geochemical and mineralogical analyses of the stratigraphic levels have yielded the following results: The basal carbonate deposits are rich in mollusks but sterile in vertebrate fossils, thus attesting to a first generalized lacustrine stage in the region, in which the micrite was precipitated under a constant, but variable in depth, water sheet (Soria et al. 1987), in a shallow and well oxygenated environment, since it is suggested by the absence of both pyrite and carbonate facies rich in organic matter that the lake was not subject to eutrophic conditions (Wells 1983). The fossils of terrestrial vertebrates preserved at Venta Micena are located exclusively above the calcere level, which is interpreted as being a paleosol, developed on the surface of the micrite sediments previously deposited during the first lacustrine stage. The distribution of fossils follows the pre-existing limnic microtopography. This surface defines a stratigraphic unconformity, which was developed after a period of generalized retraction of the Pleistocene lake (Gibert et al. 1992). The calcere paleosol thus indicates the emergence of the micrite deposits, which were then exposed to subaerial paedogene-

sis in an arid climate with high evaporation rate (Plaziat 1984). The low percentage of iron oxides (0.6% Fe₂O₃) suggests that these sediments were hardly affected by the oscillations in the phreatic level.

The Pleistocene lake of Orce had rather limited dimensions both in expanse and depth during the lacustrine stages described above, since the carbonate deposits are restricted in the large lakes to the borders, while in those of minor size they can extend over all the bottom (Kukal 1971), as happened in the studied region (Vera et al. 1985; Soria et al. 1987). The traditional connection between lakes, swamps and calcere/sebkha (which may be masked by subaerial paedogenesis of marshy and lacustrine deposits, in which the evaporation plays an essential role and modifies the original sediments; Plaziat 1984) is transformed in the Orce-Venta Micena sector in the following sequence: swamps (Plio-Pleistocene), lake (lacustrine stage 1, lower Pleistocene), emergence and swampy ponds (paleosol formation; stratigraphic unconformity), lake (lacustrine stage 2) (Arribas 1995). In this case the calcere type paedogenesis does not hide the sedimentary origin of the studied stratum, but allows the distinction of various sedimentary environments and to identify the inner surfaces which have chronological utility in the region, one of which is the local isochron of Venta Micena (Arribas et al. 1994).

**GEOCHEMICAL ANALyses AND DIAGENETIC SETTING**

Geochemical analyses have been performed on bony samples obtained from ten metacarpals of *Equus altidens* which were unearthed in different grids of the Venta Micena quarry. The samples (VME-1 to VME-10) were removed from the cortical bone at half of the diaphysis. Three samples of sediment (Fig. 2), obtained from the bottom of the fertile level of the Venta Micena stratum (VMSED-1, lacustrine stage 2), from the calcareous scab (VMSED-2, emerged environment) and
from a calcareous nodule (VMSED-3, ponds) were also analysed.

The mineral phases (Fig. 3) which predominated in all the bony samples analysed were fluorine-apatite (0-79%) and carbonate-apatite (0-81%); chlorine-apatite was detected in two samples (VME-2, 4; 24 and 47%, respectively) and hydroxyapatite in another three (VME-3, 6, 10; 26, 46 and 13%, respectively). Calcite was found in low percentages (2-16%) in all samples, except VME-10, in which this mineral was very abundant (73%). The prevailing oxides were CaO (46-49%) and P₂O₅ (20-33%); SiO₂ was found in low proportions (0-5-2%), TiO₂ was only present in four samples (VME-4, 5, 6, 8) in very low proportions (0-01-0-05%). K₂O was detected in two samples (VME-7, 8; 0-02 and 0-01%, respectively), Fe₂O₃ was present in all of them but in minor proportions (<0-4%) and MnO was absent. The predominant trace elements were Sr (2243-4198 ppm) and Ba (121-1348 ppm), followed by V (2-39 ppm), Cu (13-19 ppm), Cr (2-12 ppm), Th (1-11 ppm), Ce (0-10 ppm), Co (0-7 ppm), Ni (0-2 ppm) and La (0-2 ppm).

The comparison between the geochemical results obtained from the fossil samples and those from the sediment ones (Fig. 4) revealed the following differences and similarities:

Mineral composition: the three samples of sediment showed great mineral homogeneity (98-99% calcite, 1% quartz), and the sample from the calcreous paleosol also presented dolomite (1%) as a new mineral phase. On the contrary, the mineralogy of the samples obtained from equid fossils was more heterogeneous, since although both the fluorine-apatite and the carbonate-apatite were the prevailing mineral phases, another three phosphatic mineral phases such as carbonate-fluorine-apatite, chlorine-apatite and hydroxyapatite were also present, as well as low proportions of calcite.

Abundance of oxides: the percentages in weight for oxides were similar in all the samples analysed from the sediment, showing no significant differences among them. The oxide content of the fossil samples was also homogeneous, with the exception of VME-9 and VME-10, in which P₂O₅ constituted about 20%, and their SiO₂ (0-5-2%) content was lower and more variable than in the sediment samples (8-9-1%).

Abundance of trace elements: the trace elements which predominated in both the sediment and the
fossils were Sr and Ba. Both elements showed similar proportions in the sample from the sediment precipitated during the second lacustrine stage, while Sr prevailed over Ba in the samples from the bottom of the fossiliferous level (calcrete paleosol), from the carbonate nodules, and from the equid fossils. Ba was detected both in the bones and in the sediment in similar quantities (121-1348 ppm and 79-1328 ppm, respectively), but Sr was less abundant in the sediment (945-135 ppm) than in the fossils (2243-4198 ppm).

Inorganic matter represents approximately 70% of bone and dentine, which is usually composed of hydroxyapatite [Ca₁₀(PO₄)₆(OH)₂], and the remaining 30% is organic matter constituted in its majority by collagen, which can also vary in its chemical composition (Franchini-Vieillet et al. 1990). The fossils from Venta Micena showed a mineralogic composition in which the original phase, the hydroxyapatite, had dissapeared in 7 out of 10 samples, and its abundance was very low in the other 3 samples. The diagenetic processes seem to have produced an enrichment in calcite of the bony structure and a chemical modification of the organic apatite into other phases of the apatite group, as a function of the higher or lower substitution of the Ca, P and OH groups by different trace elements or by oxides, which were assimilated from the surrounding sediment. P was in part replaced by Si within the bony structure, and the incorporation of this element could have been produced by chemical substitution during the diagenesis or during the life of the animals, from the silicophytolits of the herbs that they consumed. Si was not found in the bones as a mineral phase (quartz) but in minerals from the apatite group, what seems to indicate that its incorporation into the bone tissue was produced during the life of the animals. In fact, the important amount of SiO₂ detected in the micrite sediment (8.6-9.1%), which was generated by chemical precipitation of carbonates, could be due to the concentration in the sediment of the organic silica from the herbs that covered the plains surrounding the paleolake of Orce (Mendoza et al. 1993). The same interpretation is adequate for the enrichment in Sr and Ba, minor elements substituting Ca in the hydroxyapatite, which were more abundant in the fossils than in the sediment. On the other hand, several trace elements such as Rb, La, Y, Zr, Nb and Ni have been detected in the sediment, but they were hardly incorporated in the bones.

The X-ray diffraction spectra of the samples analysed and their comparison with those obtained in

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Pourcentages des phases minérales (A), poids des oxydes (B) et abondance (ppm) des éléments traces (C) dans trois échantillons de la couche de Venta Micena VMSED-1: micrite de l'étage lacustre 2; VMSED-2: calcrete de paleosol; VMSED-3: micrite d'un nodule calcaire des mares.)
Figure 5 - X-ray diffraction spectra of the samples from Venta Micena. A, comparison of the three samples of sediment with samples of pure calcite and dolomite, what shows the homogeneity in the crystallinity of the spectra from the site, as indicated by their perfect overlap. B, representation of three bone samples (VME-1 to VME-3) which show great crystalline homogeneity, compared with the spectra for the two mineral phases of the apatite group with which they show a higher similarity. C, comparison between the bone from Venta Micena (VME-1) and the dentine of equid teeth from Huéscar; both show analogous composition and similar differences with the spectra of equid dentine from the palaeontological sites at Huelago and Cullar de Baza (which have a new crystalline phase, and are very similar to each other). X-ray diffraction measurements were carried out on powdered bone and tooth samples by means of a Philips diffractometer monochromatized to Cu-k radiation (λ=1540Å). Spectres de diffraction X pour des échantillons de Venta Micena. A, comparaison de trois échantillons de sédiment avec des échantillons de calcite et de dolomite purs montrant l'homogénéité de cristallinité du spectre du site comme l'indique leur recouvrement parfait. B, représentation de trois échantillons d'os (VME-1 à VME-3) montrant la grande homogénéité cristalline, comparée avec les spectres de deux phases minérales du groupe de l'apatite avec lesquels ils montrent la plus haute similitude. C, comparaison d'un os de Venta Micena (VME-1) et la dentine de dents d'équidés de Huéscar; les deux montrent une composition analogique et des différences similaires avec le spectre de dentine d'équidés des sites paléontologiques de Huelago et Cullar de Baza (qui ont une nouvelle phase cristalline et sont très similaires entre eux). Les mesures de diffraction X sont réalisées sur de l'os en poudre et des échantillons de dents à l'aide d'un diffractomètre monochromatique Philips en radiation Cu-k (λ=1540Å).
samples from other sites in the Baza Formation of the basin (Alberdi & Ruiz Bustos 1989), show interesting results (Fig. 5). The spectrograms of the equid bones from Venta Micena are similar to the spectrum for the sample of tooth dentine obtained from equids of the middle Pleistocene site at Huéscar-1. Both spectra differ from those obtained for the tooth dentine of equids from two other sites in the basin, the upper Pliocene site at Huélag (Equus stenonis livenzovenis) and the middle Pleistocene site at Cúllar de Baza-1, whose samples are very similar. Venta Micena and Huéscar-1 are very close geographically within the carbonate Baza Formation (Vera 1970a, 1970b), while Huélag and Cúllar de Baza-1 are located quite distant (several dozens of km) from the former sites, although both belong to the same basin, and the former is located in the Guadix Formation, which shows clastic characteristics. These comparisons suggest that the mineral composition of the fossilized bony tissue (excluding enamel, which presents both structural and compositional properties clearly different from those of the bone and dentine) does not rely on the taxonomic affiliation or on the age of the fossils, but on the lithogenic characteristics and the hydrogeological evolution of the different formations in which the palaeontological sites are emplaced.

The sedimentary infilling affects only those bones which have biostratinomic fractures (spiral and longitudinal fractures, as discussed below). The bones which were preserved complete lack any sediment in their inner surface, even in those areas which are close to large nutrient foramina, what indicates that the bones were buried with the periosteum intact. The sedimentary infilling has the same micrite composition as that of the stratum, and is only present in the medullary cavity of the fractured bones, in form of small mud flows which dissipate towards the interior of the specimens. This type of infilling is not found in the complete bones.

All the major long bones which were preserved complete, show one or more diagenetic fractures, orthogonal to their longitudinal axes, which are located either at half of the diaphyses or at their ends. These fractures could have been produced following two distinct processes: during the diagenetic compaction, as a result of the superposition of some elements on others (more than 90% of the bones of the assemblage are in contact with other bones) or due to the decompression produced as a consequence of the erosion of the sediments which covered the stratum. These orthogonal fractures are in all cases delimited by bone (i.e., there is no fracture defining the end of one specimen), what helps to clarify the taphonomic state of the assemblage (accumulated, resedimented or reworked), since the finding of bone fragments, isolated and delimited by this type of fractures, would imply taphonomic reorganization (i.e., burial + mineralization + diagenetic breakage + unearthing by erosion + displacement, dispersal and/or destruction of certain bones + burial of different specimens from the same bone). When these processes take place, the bone assemblage is, at least in part, mixed diagnostically (i.e., reorganized), which precludes the possibility of making detailed palaeoecological analyses, since the bones may have different age and may come from different environments. Clearly, this is not the case here.

**BIOSTRATINOMY OF THE ASSEMBLAGE: VARIATES, PROCESSES AND AGENTS**

We have analysed different biostratinomic variates in order to characterize the macrovertebrate assemblage from Venta Micena. Previous approaches to the taphonomic study of this site (Gilbert et al. 1992; Palmqvist et al. 1992) include the comparative study of the preservational state of the surface of the bones, and the evidence of the taphonomic bias experienced by the whole assemblage, respectively. In this study we have followed in part the procedure described by Behrensmeyer (1991) for the biostratinomic characterization of vertebrate assemblages.

**DIVERSITY, SPECIES ABUNDANCE, AGE CLASSES AND SIZE ESTIMATES**

The Venta Micena collection is composed of 6453 identifiable skeletal remains of 19 macromammalian species (≥ 5 kg) and more than 10,000 undentifiable bone shafts. Table 1 summarizes the raw data on the abundance of species (NISP: number of dental and non dental identifiable specimens; NNI: minimal number of individuals; updated from Martínez-Navarro 1991, 1992a).

The palaeontological sample from this site increases each year during systematic excavations. Up to the present moment, the macromammalian assemblage is composed of 19 taxa, which belong to the orders Proboscidea, Artiodactyla, Perissodactyla and Carnivora, represented by the following families: Elephantidae, Bovidae, Cervidae, Hippopotamidae, Equidae, Rhinocerotidae, Canidae, Felidae, Hyaenidae and Ursidae. The presence of two other mammalian species of small size, the badger (Meles sp.) and the porcupine (Hystrix major), has been cited in this site, although we have found no fossil remains of the former within the macrovertebrate assemblage. The first species would indicate the presence of mustelids in the palaeocommunity, and the porcupine (which is represented by an isolated maxilla)
stands out since it could be one of the biological collecting agencies of bones.

If we compare the taxonomic composition of the Venta Micena assemblage with those of another three Pleistocene lacustrine sites from the Guadix-Baza basin (Alberdi et al. 1989), we see that Venta Micena shows the highest diversity of large mammals, since each of the sites at Huelago (upper Pliocene), Huéscar-1 (early middle Pleistocene) and Cúllar de Baza-1 (middle Pleistocene) only present 10 macroamamal species. The first of these sites lacks carnivores (which constitutes an anomalous peculiarity within the palaeontological record from Spain, probably due to the special taphonomic characteristics of this site), has one proboscidean (cf. Mammutius meridionalis), two perissodactyls (Equus stenonis livensoennis and Stephanorhinus cf. eutruscus), four boids (Leptobos cf. elatus, Gazella borbonica, Gazellespira torticornis and cf. Hesperodoceras merlai), and three cervids (Cristotherium ramosus, Eucladoceros cf. senezensis and Cervidae indet.). The assemblage from Huéscar-1 has four species of carnivores (Canis eutruscus, Panthera gombaszoegensis, Homotherium sp. and Hyaenidae indet.), one proboscidean (Elephas antiquus), three perissodactyls (Equus stenonis intern. granatensis/altidens, Equus sussenbornensis and Stephanorhinus eutruscus), one cervid (Megaloceros [Mega- ceroides] cf. solilacrus) and one hippopotamid (Hipopotamus major); finally, the assemblage from Cúllar de Baza-1 has two carnivores (Canis eutruscus and Crocuta crocuta), one proboscidean (Mammuthus trogontherii), three perissodactyls (Equus altidens, Equus sussenbornensis and Stephanorhinus eutruscus), two boids (Bison sp. and Capra sp.), one cervid (Dolichodorycerus savi- ni) and one suid (Sus cf. scrofa). These three sites are also located on sediments which were deposited in swampy and lacustrine environments, under similar conditions to those of Venta Micena.
(without evidence of subaerial exposure in the assemblages). The main difference between the assemblage from Venta Micena and those recovered from other sites in the Guadix-Baza basin is the high diversity of carnivore species preserved in the former assemblage, which has all ecological niches of carnivores represented (from opportunistic scavengers to top predators). On the other hand, the taxonomic richness of large mammals in Venta Micena is the same as that recorded in a modern hyaena den (Crocuta crocuta) from the Amboseli National Park (Kenya), which was also developed on a calcareous paleosol (Hill 1981, 1984), in which the skeletal remains from 16 to 18 taxa were represented.

Table 1 shows that the herbivore species are those best represented in the Venta Micena assemblage by both NISP and MNI counts, with the following rank abundance: Equus altidens, Megaloceros (Megaceros) solilhacus, Bovini cf. Dmanisibos, Cervidae gen. et sp. indet., Soergelia minor, Hemitragus alba, Stephanorhinulus etruscus, Hippopotamus amphibus antiquus, and Mammutthus meridionalis. The worst represented species are carnivores, in which the most abundant species according to their NISP values are Pachyrcoca brevirostris and Canis (Xenocyon) falconeri (of which the hyaena stands out if we also consider its high MNI value).

The index of skeletal representation (i.e. NISP/100/[MNI]) shows that the minimal number of identifiable specimens recovered from the species i.e. NISP is the number of osseous elements found in the skeleton of a living individual of this species, and MNI is the minimal number of individuals estimated for species i.e. the assemblage) indicates for each species the percentage of skeletal elements which were preserved in relation to the sum of the total number of elements for all individuals identified in the assemblage (i.e., preservational completeness), and thus provides information about the extent of the taphonomic biases which affected the composition of the assemblage. For example, if an assemblage was produced by a catastrophic or mass mortality event, followed by immediate burial, the i.e. index would then take the maximum value (100%) for each species, since all skeletal elements would have been preserved if the diagenetic conditions were not destructive. However, the species in Venta Micena are represented by less than 20% of potentially preservable elements (Fig. 6). The herbivore species may be in order by decreasing i.e. values as follows (Table 1): Equus altidens, Bovini cf. Dmanisibos, Megaloceros (Megaceros) solilhacus, Soergelia minor, Hemitragus alba, Cervidae gen. et sp. indet., Stephanorhinulus etruscus, Hippopotamus amphibus antiquus, Mammutthus meridionalis and Praeovibos sp. The main difference between this ordering and the previous one is that the individuals of Bovini cf. Dmanisibos are better represented by skeletal remains than those of Megaloceros, although the latter species has higher NISP and MNI values, and the same difference is found between Hemitragus and Cervidae indet., respectively. Carnivores are poorly represented in the Venta Micena assemblage, since most of these species have <5% values in the i.e. index, with the exception of the fox (Vulpes praeglacialis) and the large could (Canis [Xenocyon] falconeri), which are represented mainly by cranial elements.

The age estimated for the individuals preserved in the assemblage has been classified within two major groups: immature or juvenile individuals with deciduous teeth, and adults with fully erupted permanent dentition. Inspection of data in Table 1 on the distribution of each species by juvenile and adult individuals reveals that: the species of largest body size (elephant, hippo and buffalo) are mainly represented by juvenile individuals, with the exception of the rhino; the species which are better represented by their NISP and MNI values (horse and large deer) also show high percentages of juvenile individuals (>40%); the carnivore species are represented exclusively by adult individuals, with the exception of the hyaenid and the ursid (40% of the individuals of Pachyrcoca brevirostris are juveniles, which are represented by deciduous teeth not isolated from the maxilla or mandible, which indicates that these cranial ele-

![Figure 6 - Index of representation (Ie: percentage of preserved skeletal elements in relation to the original number of bones estimated from MNI counts) for the species of large mammals identified at Venta Micena. Indice de présence (Ie: pourcentage d'éléments squelettiques préservés en fonction de nombre estimés d'os par décompte MNI) pour les espèces de grands mammifères identifiées à Venta Micena.](image-url)
ments were not produced by tooth replacement, but as a consequence of the death of very young individuals).

Body weights (W, in kg) for adults of each species (mean and range) were calculated from several regression equations of weight on craniomandibular/postcranial variates in recent species (Janis 1990; Roth 1990; Scott 1990; Van Valkenburg 1990). The mean value estimated for each species and the widest range of weight estimations (i.e., the minimum and the maximum of all values obtained with these regressions for craniodental and postcranial remains of a given species) have been included in Table 1. These estimates indicate that the Venta Micena assemblage comprises species weighing between 3-5 kg (fox) and 6000 kg (elephant, approximated range: 3500-10,000 kg), which constitutes a total range of body sizes in the palaeocommunity of more than three orders of magnitude.

**BONE ORIENTATION, SPATIAL DENSITY AND SKELETAL ARTICULATION**

The distribution in a rose diagram of the directions of the longitudinal axes of long bones in Venta Micena shows no preferred orientation or alignment (Gibert & Caporiccio 1989), which suggests a random pattern in the distribution (Shipman 1981). However, two factors must be borne in mind in the analysis of bone orientation: the presence of a water sheet in the environment in which the assemblage was accumulated, and the fact that the skeletal elements could or could not experience free movements aligning with the direction of the currents (as a function of bone density and size, type of depositional interphase, microtopography, grain size and sediment density; Friisn & Todds 1986). In Venta Micena the stratigraphic evidence indicates the absence of channelled currents in the area in which the site was formed, which was the plains that surrounded a lake, with numerous ponds emplaced on a paleosol where the majority of the fossils were concentrated. The marked microtopography, with height differences of up to 40 cm, must have determined the position of the bones on the substrate, as well as their possibilities to be displaced by water currents (of which there is no objective evidence in the sediment) or by trampling. Therefore, the bones at Venta Micena had fewer opportunities to experience free movements, since their position is determined by the geomorphology of the palaeorelief and the high density of osseous elements preserved in the site, which form an intricated mixture which is very difficult to excavate. The absence of preferred orientations in the bone assemblage is thus determined by the original characteristics of the substrate.

As was explained before, the concentration of bones in this site is very high, and more than 90% of the skeletal elements are in contact with other elements (Fig. 7). The assemblage shows a low degree of horizontal dispersion, with groups of disarticulated but associated elements (i.e., skulls with mandibles, metapodials and phalanges), which represent 80% of all bones, and groups of articulated elements in a lower proportion (approximately 20%). The articulations more frequently preserved are those formed by tibiotarsal-metatarsal-phalanges, humerus-radius-ulna, radius-carpal-metacarpal-phalanges and articulated vertebrae.

The Venta Micena site has provided a large amount of skeletal elements. The density plot for the distribution of fossils on the excavated surface of the quarry (number of bones and teeth recovered from each m²) shows that the mean density of elements is approximately 60/m² (Fig. 8, obtained using the SYSTAT program, version 5.0), although two well defined areas have 80 or even 90 bones/m² of up to 50 cm of length (i.e., tibiae of Equus and metapodials of Megaloceros). The number of elements per m² is in part a function of their size, since the density of elements reaches higher values in the squares which show a majority of postcranial bones (2-50 cm length), while the spatial density is lower in those squares in which cranial elements (60-80 cm length) predominate, because they have greater surface and volume than the former bones, although the surface of these squares is also almost completely covered by fossils.
FIGURE 8 - Density plot for the abundance of skeletal remains (number of bones and teeth per square meter) in the Venta Micena excavation area. Plan de densité pour l'abondance des restes squelettiques (nombre d'os et de dents par metre carré) sur la surface excavée de Venta Micena.

REPRESENTATION OF SKELETAL PARTS AND BONE MODIFICATION

The palaeontological collection recovered from Venta Micena is composed of 6453 identifiable skeletal elements of large mammals, in which all range sizes of complete elements and bone fragments are represented (i.e., from premolars and third phalanges of *Vulpes* to complete mandibles of *Mammuthus*). Fossil remains of micromammals, including teeth and elements from the axial skeleton, are also present in this site, although their study is not included in this work.

Descriptive taphonomic analysis of the Venta Micena assemblage was based on a well restored sample of 1339 specimens housed at the Museum of Paleontology of Orce, which represents a random sample of the Venta Micena collection (Palmqvist et al. 1996a). Isolated teeth represent 12.5%, and 1.4% are fragments of deer antlers. In the sample of bone remains (N = 1152; Fig. 9), limb bones dominate (64.7%), followed by vertebrae (15.5%), cranial elements (10.4%), phalanges (6.3%), and ribs (3.1%). The most abundant post-cranial bones (Fig. 10) are metapodials (>20%), tibiae and humeri (6-8%), calcanei and astragalii (3-5%), escapuli, radii, femori, first and second phalanges (2-3%), pelvis fragments and third phalanges (4.3%), and ulnae (<1%). Scapuli are basically represented by proximal fragments; fragments of diaphyses predominate among fossil humeri; the most complete elements are radii; femori are mainly represented by fragments of diaphyses and tibiae by distal epiphyses; the pelvis is only represented by fragments which preserve the acetabulum (Fig. 11).

FIGURE 9 - Representation of different types of bones in the Venta Micena equid and in the assemblage of large mammals (shaded area: abundance of these elements in a horse skeleton), compared with data obtained from six modern dens of Crocuta (Timbavati, South Africa; Brain 1981). Représentation des différents types d'os de l'équidé de Venta Micena dans l'assemblage de grands mammifères (surface hachurée: abondance de ces éléments d'un squelette de cheval), comparée avec les données obtenues pour six repaires modernes de Crocuta (Timbavati, Afrique du Sud, Brain 1981).

The surfaces of the bones seem to have been exposed to the effects of subaerial weathering for a short time: 89.3% of the skeletal elements show weathering stage 0 (Behrensmeyer 1978), and only 10.7% of the bones (of which two thirds are metapodials) present weathering stage 1, with few, shallow and small split line cracks due to insolation (1-8 in each bone), and without flaking of their outer surface. These results indicate that subaerial weathering was relatively unimportant.
The bones which were preserved complete, lack sedimentary filling, even in those areas of the medullary cavity which are close to nutrient foramina, which indicates that the bones were buried with the periosteum intact. Figure 12 shows the distribution of percentages of bones per weathering stages in Venta Micena and in several control bone assemblages and carcasses of known age since death (Behrensmeyer 1978; Gifford 1977, 1984). The position of Venta Micena in this diagram is close to those of the least weathered assemblages, thus indicating a very short period of subaerial exposure before burial (<1 year).

Horse (E. altidens) remains (N = 457) are not well dispersed horizontally; groups of articulated elements represent nearly 20% of this sample, and the remaining 80% of non-articulated bones are found...
associated. Biostratinomic fractures are abundant (Figs 13-15); only 29.1% (73/251) of major long bones are complete (most of them metapodials), and Type II spiral fractures (Shipman 1981; Lyman 1994) are predominant (100% of fragmented humeri, femurs and radii, 74.4% of tibiae); other types are longitudinal fractures (25.6% of tibiae), undifferentiated fractures (all ribs and vertebrae, with the exception of several vertebrae which only lack their apophyses) and isolated maxilla with both cheek tooth rows (33.3% of cranial elements). On the one hand, the outer surface of the bones is well preserved: no one bone shows signs of abrasion or polish (with the exception of four out of six petrosus bones), and only four elements of the sample (0.9%) are slightly dissolved. On the other hand, gnawing marks are very frequent (Figs 16-18): all cranial fragments, scapuli, humeri, radii, pelvis, femori and tibiae show striations and biting marks produced by carnivores, the preserved epiphyses have furrows and punctures, and the diaphyses, as well as the skull bones, show scoring and pitting. These marks are also observed in all other taxa identified at Venta Micena. Coprolites are relatively common in Venta Micena, preserved as isolated lobes with diameters between 3 and 6 cm.

The results presented up to this moment, allow us to deduce that the very rich and diverse palaeontological site at Venta Micena was formed in the dessicated border of a lake, and that the geological agents may be excluded from the bone accumulation process. The geochemical data from the samples obtained in the sediment and in the fossils, as well as the diagenetic information obtained from the analyses of the fossils, are both in keeping with each other, thus corroborating the initial impression that the assemblage represents an accumulated taphonomic stage, without objective evidence of taphonomic reworking. The bone assemblage is composed of demic palaeobiological entities (hyaenids, as it will be shown later) and autochthonous preserved entities (the remaining species), which were recorded in situ (sensu Fernández-López 1991). The results obtained in all biostratinomic analyses indicate clearly that this assemblage shows a differential bias in the representation of certain anatomical parts and bones in relation to others, and that the accumulation of bones was generated by the activity of scavenger carnivores, presumably hyaenids, being buried in a short period of time.

QUANTITATIVE TAPHONOMY

The quantitative taphonomic study of the Venta Micena assemblage was based on three different approaches: the analysis of size/abundance pat-
terns in the ungulate species using the model proposed by Damuth (1982); the analysis of the abundance of preserved epiphyses and complete major long bones of ruminants in the assemblage, and; the study of bone frequencies in the assemblage in comparison to some recent and archaeological deposits accumulated by carnivores, rodents and hominids.

ANALYSIS OF SIZE-ABUNDANCE PATTERNS

In a fossil assemblage taphonomically unbiased, the abundance of skeletal remains for a given species will depend exclusively on the number of individuals that died while the assemblage was being formed. The relative abundance of each species (A) is estimated as a function of both its mean population density (D) in the palaeocommunity and its population turnover rate (T): A = f(D, T) (Damuth 1982).

Several studies (Damuth 1981, 1987, 1991; Peters 1983; Calder 1982, 1984) have shown that population density (number of individuals per unit area) of a species is inversely and allometrically related to body weight (W) by a slope close to the -0.75 power:

D = K.W^{-0.75}.

With respect to the population turnover rate, related parameters as the birth rate, the duration of postnatal growth or the reciprocal of life expec-
tancy at birth (Western 1979, 1980; Damuth 1982; Peters 1983; Calder 1982, 1984) are allometrically related to species body size, with a slope of around 0.3:

\[ T_r = K \cdot W^{0.3} \]

As a function of both equations, the original abundance \( A \) of bones from the different species present in a fossil assemblage is determined by:

\[ A = \frac{D \cdot T_r}{T} = K \cdot W^{0.17} \cdot K \cdot W^{0.3} = K \cdot W^{1.00} \]

with a 95% confidence interval for the slope ranging between -0.8 and 1.3 (Damuth 1982).

If the value of the slope that relates \( A \) with \( W \) in a fossil assemblage is included within this interval (-1.05 ± 0.25), it could be then concluded that the assemblage had not experienced significant taphonomic biases with respect to the quantitative composition of the original paleonicoenose, and that the community structure was preserved during fossilization. If, on the contrary, the value obtained for the slope lies well outside the confidence interval, it should be then deduced that the relative frequencies of the species represented in the bony accumulation do not fit the size/abundance relationship that characterizes recent communities, and that the original composition of the
assemblage was then biased by taphonomic processes (or by other factors, such as sampling or curating errors).

Body size is one of the factors that seems to have the greatest influence on the fossilization potential of terrestrial vertebrates (Behrensmeyer et al. 1979; Behrensmeyer & Dechant Boaz 1980; Damuth 1982), since the bones of large-bodied species are more resistant to processes of physico-chemical weathering and biological destruction (i.e., exposure to sun radiation, salt precipitation, changes in relative humidity, trampling by ungulates, carnivore gnawing, root growth, etc), due to their smaller relative surface (the ratio of their outer surface to the enclosed volume). To correct for taphonomic loss due to these processes during the period when the bones were exposed on the surface before their definitive burial, the value \( d = 0.68 [\log(W_a) - \log(W_i)] \) should be calculated, where \( W_i \) is the body weight estimated for species \( i \), and \( W_a \) is the weight of the largest species in the assemblage. In this way, the amended original abundance (\( A^o \)) of each species will be estimated (Damuth 1982) as:

\[ \log(A^o) = \log(A) + d. \]

Before the model can be used for the quantitative taphonomic analysis of the Venta Micena palaeocommunity, some considerations are in order. Firstly, the analysis must be restricted to a single trophic level, since the population densities decrea-
se for a given body size as height in the energetic or ecological pyramid increases. Primary consumer species are, as a rule, the most suitable for this analysis, since they are abundant in communities, are highly diverse, and differ considerably in size (at least two orders of magnitude in size differences are necessary to obtain a statistically reliable fit to the model). In the Venta Micena assemblage 5558 dental and non-dental remains have been identified from 11 species of herbivorous macromammals, whose estimated weights range from approximately 8 to 6000 kg. Carnivores are less relevant for this analysis, as a function of their scarcity in the original communities and, as a consequence, in the fossil
assemblages (264 remains in Venta Micena, corresponding to 8 species ranging in body weight from 5 to 375 kg), which increases the randomness of their sampling (Wolf 1975; Palmqvist 1991, 1993; McKinney 1996). Secondly, the total number of skeletal remains (NISP) of each species is the best estimate of its abundance (A) in the assemblage, since the counts of minimal number of individuals (MNI) tend to decrease the values of the common species and to overestimate those of rare species. Thirdly, analysis of only part of the assemblage is still valid, and species about which there is some uncertainty (such as would result from our inability to consistently identify their specimens) may be omitted.
from the analysis with no loss of accuracy (Damuth 1982).

The values of Log(A) and Log(W) for the Venta Micena herbivore species (N=9) are shown in Figure 19A, in which the regression line obtained for both variates using for the adjustment the least squares method is also included. Two species were excluded from the analysis: Praeovibos sp., a mountain-dwelling species is poorly represented in the assemblage, given that it was clearly allochthonous to the palaeocommunity; Caprini indet. is represented by only one distal epiphysis of a metacarpal. The fit obtained in the adjustment is statistically significant at the 95% confidence level, but the slope is not included within the range of values anticipated by Damuth's model: (1.05 ± 0.25):

Log(A) = 9.448±1.626 - 0.598±0.253 Log(W); r = -0.665, F = 5.564 (p < 0.05).

In contrast, when we analyse the values for corrected abundance (A*) of the species in the absence of taphonomic biases (Fig. 19B), the fit obtained is statistically significant at the 99.9% confidence level, and the slope is within the range of values predicted by the model:

Log(A*) = 15.367±1.626 - 1.278±0.253 Log(W); r = -0.885, F = 25.422 (p < 0.001)

These results confirm that the main loss of information during the taphonomic history of the Venta Micena assemblage was due to destruction of skeletal remains during the period when the bones were exposed on the surface before their definitive burial, and that the effects of this information loss were greater in species of smaller body size, thus biasing their quantitative representation in the fossil assemblage.

ABUNDANCE OF EPİPHYES AND COMPLETE MAJOR LONG BONES

Two factors seem to have a substantial influence on the frequencies of skeletal parts in an untrans-
Figure 19: Relationship between body weight (W, in kg) and abundance of skeletal remains (A: original abundance = NISP; A*: abundance corrected for taphonomic biases) in the ungulate species (N = 9) of the Venta Micena assemblage (A: regression line obtained for A vs. W, adjusted by minimum squares analysis; B: regression line for A* vs. W). a, Hemitragus alba; b, Cervidae gen. et sp. indet.; c, Soergelia minor; d, Equus altidens; e, Megaloceros (Megaceroides) sollihageni; f, Bovini cf. Omasius; g, Stephanorhinus etruscus; h, Hippopotamus amphibius antiquus; i, Mammutthus meridianalis. Relations entre le poids corporel (W en kg) et l'abondance des restes de squelettes (A: abondance originelle = NISP; A*: abondance corrigée des biais taphonomiques) pour les especes d'ongulés (N = 9) de l'assemblage de Venta Micena (A: droite de regression obtenue pour A vs. W, ajustee par l'analyse des carrés minimaux; B, droite de regression pour A* vs. W).

ported assemblage (Binford 1978, 1981; Binford & Bertram 1977; Blumenshine & Madrigal 1993; Lyman 1984, 1994): structural density of bones and within-bone nutrient utility. Overall meat/bone utility plus ease of disarticulation are also important factors affecting skeletal part representation in accumulations transported by carnivores (see Lyman 1994, and references therein). Several taphonomic processes, such as carnivore damage (Marean & Spencer 1991), are mediated by the structural density of bones (mechanical and chemical attrition have greater effects on bones with low bulk density), and by the extraction of nutrients within bones, particularly marrow. Many structural density estimates, obtained using photon absorptiometry, are available in the literature (see Lyman 1994), but the estimation of within-bone nutrients is rather problematic. Interspecific differences in the distribution of flesh between the hindlimb and forelimb of bovids seem to be related to locomotor type (Blumenshine & Caro 1986). In a similar way, absolute long bone marrow yields differ among species, and among individuals of different size within a species. Most published data (Binford 1978; Blumenshine 1991; Emerson 1990; Jones & Metcalfe 1988) are clearly inadequate for assessing this variability. Only Blumenshine and Madrigal (1993) have addressed this issue, using a broad sample of East African ungulates.

Figure 20 shows the abundance of long bone epiphyses of ruminants in the Venta Micena assemblage and their mean bone mineral density (estimated from values obtained using photon absorptiometry in modern bison and deer; Lyman 1994). The positive relationship observed between both variates is statistically significant, according with a least squares regression adjustment:

\[ \text{Abundance} = -68.522(\pm23.007) + 270.841(\pm56.458) \text{Density;} \quad r = 0.835, F = 23.01 \ (p < 0.001). \]

Similarly, Marean & Spencer (1991) found a strong correlation between the frequencies of long bone parts of domestic sheep that survived grazing by spotted hyaenas and their structural density.

Figure 21 shows the abundance of major long bone epiphyses of ruminants and their mean fat content (estimated from values for moder bison in Brink 1997). The inverse relationship detected between both variates is also very significant, according with a least squares regression adjustment:

\[ \text{Abundance} = 70.086(\pm7.665) - 0.249(\pm0.051) \text{ Fat weight;} \quad r = -0.839, F = 23.71 \ (p < 0.001). \]

However, the structural density of the bone is inversely related with its fat content, which is higher in those epiphyses in which the less denser, cancellous tissue predominate. Figure 22 shows a plot of density and fat content of epiphyses (x and y-axes), where the abundance of long bone epiphyses is represented by contour lines (z-axis) using 20 intervals of increasing value. A multiple regression approach to the estimation of epiphyses as a function of both their density and fat content has shown a statistically significant relationship:

\[ \text{Abundance} = 0.706(\pm5.438) + 138.176(\pm117.883) \text{Density - 0.137}(\pm0.108) \text{ Fat weight;} \quad r = 0.862, F = 13.002 \ (p < 0.002), \]

in which the fat content of the epiphyses is a somewhat better predictor of their abundance, as
it may be deduced from the values of the standardized coefficients (0.428 and -0.460 for bone density and fat content, respectively). This is confirmed by the values obtained for the first order partial correlation coefficient of the abundance of epiphyses on their estimated structural density being constant their fat content ($r = 0.363$), and of the abundance of epiphyses on their fat weight with independence of their density ($r = 0.390$).

The abundance of major long bones of ruminants in Venta Micena (complete limb bones and long bone cylinders, lacking one or both epiphyses) and their mean wet weights of marrow content (estimated from values for modern wildebeest in Blumenschine & Madrigal 1993) is shown in Figure 23. There is an inverse relationship between the abundance of each long bone and its marrow content, which is linearized by means of logarithmic transformation as:

$$\text{Log(Abundance)} = 9.249(\pm 0.819) - 2.033(\pm 0.248) \text{Log(Marrow content);}$$

$$r = -0.972, F = 67.29 (p < 0.001).$$

These results indicate the preferential consumption by hyaenas of low-density skeletal parts, dif-
ferential fragmentation leading to less dense bone parts being crushed into unidentifiable fragments in contrast to denser bone parts simply broken into small but recognizable pieces during the extraction of marrow (Lyman 1994). The selective transport of certain anatomical parts and the preferential breakage by hyaenas of the richer marrow bones were thus major factors biasing the composition of the Venta Micena assemblage.

We can evaluate the extent of this taphonomic bias, which affected the original composition of the Venta Micena assemblage, by comparing the abundance of ruminants and equids which may be deduced from the number of complete metapodials, the most abundant major long bones preserved complete in the fossil assemblage, with the raw abundance of both groups of ungulates, which is easily estimated using MNI counts obtained from dental elements (Table 1). Ruminants are represented in Venta Micena by 87 metapodials, complete or long bone cylinders lacking only one epiphysis (44 metacarpals and 43 metatarsals), and equids by 136 metapodials (60 metacarpals and 76 metatarsals). The ratio of ruminants to equids is thus 0.640 (87/136, approximately 1 ruminant: 1.6 equids). However, ruminants are represented in the assemblage by a higher MNI (111) than equids (70), with MNI estimated from teeth counts, and the ratio is therefore 1.586 (111/70, approximately 1 ruminant: 0.6 equids). Both estimations differ widely, but the latter is the most reliable of them, given that we expect no great differences in fossilization potential of teeth from ruminants and equids, while the preservation of complete long bones is highly biased by differential gnawing and fragmentation by hyaenas as a function of their structural density, fat and marrow content, as it was demonstrated before (Figs 20-23).

Total marrow yields of equid bones are on average five-fold smaller than those from ruminants (Blumenshine & Madrigal 1993): specifically, the mean weight of marrow content from the metapodials of Burchell's zebra is 0.22 g, while this estimate is of 14.22 g for wildebeest metapodials. The Venta Micena equid (E. altidens) was similar in size to modern E. grevy, with an estimated weight of approximately 350 kg (Palmaqvist et al. 1996a). Given the fact that E. burchelli weights on average 230 kg, we can estimate by simple linear interpolation a mean marrow content of 9.47 g for the metapodials of E. altidens. This means that one
metapodial of the Venta Micena equid had 1,503 times less marrow content than a metapodial of ruminant (the ruminant species identified in the assemblage range in body size from 8 kg for Caprini indet. to 450 kg for Bovini cf. Dmanisibos; the estimation of 14.23 g for the metapodials of modern wildebeest, a species with a body weight of 170 kg, is thus appropriate as an average for all ruminants preserved in the fossil assemblage).

Using the equation that relates the abundance of complete long bones with their marrow content [log(abundance) = 9.249 - 2.033 log(marrow weight)] it is possible to predict that a decrease by a factor of 1,503 in the mean marrow content of a given long bone would translate in an increase by a factor of 2,290 of its abundance in the assemblage; in other words, if the mean marrow content of the ruminant metapodials would have been similar to that of the equid ones, the abundance of the former in the assemblage should be of approximately 199 complete elements, instead of 87. This figure gives a ratio of ruminants to equids of 1.463 (199/138, approximately 1 ruminant: 0.7 equids), which is very close to that calculated from MNI counts (1 ruminant: 0.6 equids), and thus confirms that differential fragmentation by hyaenas was the major factor biasing the representation of ruminant post-cranial bones in Venta Micena.

MULTIVARIATE ANALYSIS OF BONE FREQUENCIES

To determine the agents that were mainly responsible for the initial accumulation of bones at Venta Micena, we compared known frequencies of different types of postcranial bones in various fossil and recent assemblages (Table 2). This comparative database includes bones exposed on the surface or partially buried in Amboseli National Park (Kenya), assemblages found at open feeding-places of several carnivore species, those from dens and lairs used by leopards, hyaenas and porcupines, and also the bones present in both recent human camps and archaeological assemblages. Bones were clustered in four groups (I: vertebrae;
II: ribs; III: limb and girdle bones; IV: phalanges) to facilitate comparisons between data from different bibliographic sources (many of which included complete lists, with the abundance of each skeletal element, but in several references the bones were already clustered in groups similar to those used here). The teeth, cranial elements and hemimandibles were excluded from the analysis, as their frequencies were highly variable (depending, for example, on whether hyaenas could or could not fracture the skulls), and such elements did not show any characteristic pattern that allowed discrimination of assemblages.

Figure 24 illustrates the results obtained in a correspondence analysis of the frequencies of the four types of bones (groups I-IV) in these assemblages. This multivariate statistical method was used because it is the most suitable for data on frequencies such as those in contingency tables (Reyment & Jöreskog 1993). The two first correspondence axes explain more than 95% of the original variance. The assemblages we analysed show a parabolic or horseshoe distribution in the bivariate scatter-plot for correspondence axes I and II (Guttman effect), which expresses a quadratic relationship between the latent vectors and indicates, among other things, a strong gradient in the frequencies of the different types of bones. The first factor is directly correlated with the abundance of vertebrae and ribs, the least persistant bony elements, with higher factor scores corresponding to assemblages in which these elements are predominant (bones exposed on the surface of Amboseli Park, in open carnivore feeding-places, in the porcupine lair and in the hunter-gatherer camp). This axis is inversely correlated with the frequencies of both phalanges and limb and girdle bones, elements that are more abundant in the remaining assemblages. The

<table>
<thead>
<tr>
<th>Assemblages</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>N</th>
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<td>35.7%</td>
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<td>13551</td>
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<td>9.5%</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>3 Brown and spotted hyaenas</td>
<td>35.7%</td>
<td>23.3%</td>
<td>35.5%</td>
<td>10.5%</td>
<td>1089</td>
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<tr>
<td>4 Lions</td>
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<td>39.8%</td>
<td>17.0%</td>
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<td>17.2%</td>
<td>41.7%</td>
<td>17.9%</td>
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<td>6 Jackals</td>
<td>26.1%</td>
<td>15.6%</td>
<td>40.7%</td>
<td>17.8%</td>
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<td>7 Leopards</td>
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<td>25.2%</td>
<td>4.9%</td>
<td>40.5%</td>
<td>29.4%</td>
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<td>9 Spotted hyaenas</td>
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<td>76.3%</td>
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<td>5.5%</td>
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<td>1.5%</td>
<td>76.2%</td>
<td>11.6%</td>
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<td>0.0%</td>
<td>90.8%</td>
<td>2.2%</td>
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<td>Kerbis-Petershan &amp; Kolka-Horwitz</td>
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<td>0.7%</td>
<td>92.2%</td>
<td>2.4%</td>
<td>295</td>
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<td>15 Indet. hyaena den</td>
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<td>5.0%</td>
<td>67.5%</td>
<td>6.3%</td>
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<td>0.7%</td>
<td>84.5%</td>
<td>12.2%</td>
<td>2139</td>
<td>Klein &amp; Cru-Uribe 1984</td>
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<tr>
<td>17 Porcupines</td>
<td>35.9%</td>
<td>5.9%</td>
<td>49.9%</td>
<td>8.3%</td>
<td>726</td>
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<td>18 San hunter-gatherer camp</td>
<td>30.1%</td>
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<td>41.1%</td>
<td>9.0%</td>
<td>601</td>
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<td>22.5%</td>
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<td>57.8%</td>
<td>10.7%</td>
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<td>10.6%</td>
<td>49.9%</td>
<td>10.9%</td>
<td>4083</td>
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<td>22 Upper Pleistocene cave at Boeplaas</td>
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<td>5.3%</td>
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<td>4.1%</td>
<td>44.4%</td>
<td>48.7%</td>
<td>2324</td>
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<td>54.7%</td>
<td>22.6%</td>
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<td>25 Lower Pleistocene Site at Venta Micena</td>
<td>9.3%</td>
<td>5.0%</td>
<td>79.3%</td>
<td>6.4%</td>
<td>3268</td>
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<td>6.4%</td>
<td>79.5%</td>
<td>5.3%</td>
<td>342</td>
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<td>27 FxO20 level at Koobi Fora</td>
<td>42.7%</td>
<td>8.8%</td>
<td>47.4%</td>
<td>1.1%</td>
<td>654</td>
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<tr>
<td>28 FLK Zinganthropus Site level 22 at Olde</td>
<td>38.7%</td>
<td>17.4%</td>
<td>43.5%</td>
<td>2.6%</td>
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<td>33.6%</td>
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<td>35.7%</td>
<td>9.3%</td>
<td>571</td>
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<tr>
<td>30 FLK North level North level 2 at Oldevai</td>
<td>23.8%</td>
<td>6.0%</td>
<td>58.9%</td>
<td>11.3%</td>
<td>302</td>
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</table>

TABLE 2 - Relative frequencies of four types of postcranial bones (I: vertebrae; II: ribs; III: limb and girdle bones; IV: phalanges) in several fossil and recent assemblages. N: total number of bones in each assemblage. Fréquences relatives de quatre types d’os postcrâniens (I: vertèbres; II: côtes; III: os des membres et des os centures; IV: phalanges) de plusieurs assemblages fossiles et actuels. N: nombre total d’os dans chaque assemblage.
The second factor shows higher projections for bone accumulations in which long bones are well represented, essentially those from spotted and striped hyaena dens, as well as those from the Hotspot camp (in which there are joint effects of *Homo* and *Canis* on bones), whereas negative values correspond to bone accumulations showing higher raw frequencies of phalanges (some assemblages accumulated by the man in caves from upper Pleistocene times, as well as from leopard dens).

The distribution of bone assemblages collected by the two main collecting agents (hominids and hyaenids) show quite different behavior: hyaenid accumulations are more homogeneous in composition (Table 2), since they consist mainly of group III skeletal elements (limb and girdle bones, excluding phalanges), whereas other types of bones are scarce in them. The greatest difference among the assemblages which were collected by hyaenas is found between dens of striped hyaenas (which are mainly carrion eaters due to their smaller size and solitary habits) and those of spotted hyaenas (whose larger size and strong social organization make them efficient hunters). In the former bone assemblages, ribs and vertebrae are almost absent, whereas in the latter ones these elements are somewhat more abundant, thus denoting less full utilization of the carrion. Contrariwise, the composition of bone assemblages due to anthropic action is more heterogeneous, and varies considerably depending on whether they derive from settlements established in an open camp or in a cave.

Venta Micena lies in the region of the factorial diagram occupied by the bone assemblages originating from spotted hyaena dens. With respect to the African Plio-Pleistocene assemblages analyzed here, all with purported patterns of anthropic activity on bones (Bunn 1982), the level FxJ50 of Koobi Fora (main-east) is also included within the group of hyaenid-collected assemblages, close in position to Venta Micena, whereas level FxJ50 from Koobi Fora and Olduvai levels FLK 6 and 22 ("Zinjanthropus" site) are placed near the less-biased assemblages from open habitats. Olduvai level FLK North 2 takes an intermediate position between the two sets.

The results of the multivariate comparison suggest that the Venta Micena assemblage originated mainly through accumulation by hyaenas (*Pachycrocuta brevirostris*) at feeding places nearby their dens, of skeletal remains of the prey hunted by different carnivores. This interpretation is supported by analysis of the distribution of teeth and bones in the Venta Micena excavation quarry (Fig. 8), which shows two areas with greater abundance of skeletal remains, and which probably correspond to the bones dispersed at the entries of shallow dens, whose original structure was not preserved due to the sedimentary characteristics of the stratum and the diagenetic compaction. The recovery of relatively high numbers of deciduous teeth of *P. brevirostris* reinforces this hypothesis (as other carnivores are represented in the assemblage only by adult individuals) and helps to reject the possibility that bones
were accumulated in open feeding-places located at hunting sites distant from dens, since it can be presumed that infant individuals would not accompany adults on their hunts, but would stay near the dens, as occurs in modern spotted hyaenas (Kruuk 1972).

A MODEL OF PREY SELECTION

Four types of evidence strongly support a selection of prey by carnivores at Venta Micena during lower Pleistocene times (Palmqvist et al. 1996a): the interspecific analysis of the abundance of remains of juvenile individuals among ungulates, in relation to the average weight estimated for adults in each species; the U-shaped attritional mortality profiles deduced from crown heighth measurements in several ungulate species; the presence of many metapodialis showing osteopathologies such as arthrosis, and; the sex ratio deduced from the metapodials of buffalos and equids, which is in both cases biased in favour of females.

JUVENILE/ADULT RATIOS

MNI counts for each species in the Venta Micena assemblage are shown in Table 1, in which the numbers of young individuals with deciduous teeth (from calves to subadults or yearlings) and of adults with fully erupted permanent dentition are given. The percentage of juvenile individuals for each ungulate species, in relation to the mean weight estimated for adults, is shown in Figure 25. Larger species are represented in the fossil assemblage by a comparatively greater MNI of juveniles than those of smaller species.

The ratio of juvenile/adult individuals in a population depends on two factors: the annual birth rate or reproduction rate, and the duration of infancy. The reproduction rate scales approximately to the -0.3 power of adult body weight of a given species (the slope for births/year ranges from -0.26 [Eisenberg 1981] to -0.33 [Western 1979, 1980]). The duration of infancy is interspecifically related to body mass by a power close to 0.3 (0.29 for the time needed to reach reproductive maturity [Calder 1982, 1984] and 0.28 for the rate of incremental growth [Case 1978]). The proportion of juvenile individuals for a given species is thus the product of annual birthrate (B) and duration of infancy (D):

\[
\%_{\text{juvenile individuals}} = B \cdot D = K \cdot W^{0.3} = K \cdot W_o = \text{constant.}
\]

This percentage will be thus approximately constant and independent of species body size. However, in the ungulate species from the Venta Micena assemblage we noted a positive relationship between the two variates, which is highly significant statistically (Fig. 25):

\[
\log(\% \text{ juveniles}) = 1.401(\pm 0.540) + 0.346(\pm 0.084) \log(\text{weight}); \ r = 0.841, P = 16.95 (p < 0.004).
\]

This result suggests strong selection by carnivores, according to the age and size of their ungulate prey, since predation of comparatively larger species such as elephant and hippo is focussed on juvenile and more vulnerable individuals, whereas in smaller species young and adult individuals are captured at similar frequencies.
MORTALITY PROFILES

Interspecific analysis of juvenile/adult ratios for ungulates in Venta Micena indicates a different age of death depending on the size of the prey, as a consequence of selection by predators, which would increase the proportion of young and more vulnerable individuals hunted of those ungulate prey species of larger body size. However, the juvenile/adult ratios have poor resolution with respect to habitual prey age selection by carnivore species. Given this limitation, mortality profile patterns were deduced for those ungulate species which show greater relative abundance in the assemblage, the horse *Equus altidens* (MNI = 70, 37.4% of the total MNI of ungulates in the assemblage) and the large deer *Megaloceros (Megaceroides) solihacus* (36, 19.3% of the ungulates). Age at death was calculated from dp4 and P4 crown height measurements (after Klein & Cruz-Uribe 1983, 1984).

The mortality curve deduced for *E. altidens* (Fig. 26A) indicates a clear U-shaped age profile, which suggests that death occurred mainly as a result of predation, and that predation was focussed both on very young individuals (most of them showing unworn dp4) and past prime adults (with medium to heavily worn P4). This pattern of mortality is similar to those observed for modern ungulate prey species hunted in a selective way by different carnivores ranging in size from the wild dog (*Lycaon pictus*) to the lion (*Panthera leo*) (Fig. 27).

The attritional profile of *M. solihacus* (Fig. 26B) shows a very pronounced peak corresponding to death in the first 10% of potential lifespan. This difference with the mortality curve deduced for the horse may be due to the somewhat greater size estimated for the former species (289-568 kg, in contrast with a range of weights for *E. altidens* of 244-487 kg). The shape of the curve for *M. solihacus* is similar to that found for Cape buffalo (*Syncerus caffer*) from the Middle Stone age layers of Klacies River Mouth Cave 1, South Africa (Klein & Cruz-Uribe 1983), which approximates an idealized attritional profile.

OSTEOPATHOLOGIES

A study of the long bones from Venta Micena have revealed many osteopathologies (Fig. 28A,B), the most frequent of which is arthrosis; it was found in the distal epiphysis of a metacarpal of a large deer (*M. solihacus*) and in two third metatarsals of equid (*E. altidens*); both cases were manifested as considerable osseous overgrowths. Another type of abnormality was present in the diaphyses of a goat metacarpal (*H. alba*) and of an equid metatarsal, both of which present a wrinkled surface with osseous accretion. A third and more subtle type of osteopathy was found in the proximal epiphysis of several horse and buffalo (Bovini cf. *Dmanisisbos*) metacarpals and metatarsals, affecting the articular facets of the metapodials, which were absent or showed abnormal growth. Results of a study of part of the Venta Micena collection indicate that these bone abnormalities are rather common: 13 out of 184 metapodials analysed of *M. solihacus*, Bovini cf. *Dmanisisbos* and *E. altidens* show signs of disease. Given that each ungulate has four metapodials, the pooled percentage of crippled animals of all three species would be approximately 28% (31% of equid, 19% of deer and 26% of buffalo). This proportion is higher than what would be expected in wild populations, and thus suggestive that such individuals in less than optimum condition were
actively selected by the predators, since these pathologies must have limited the ability of the animals to run, thus reducing their chances of escaping from predators.

SEX RATIO IN UNGULATES

A third line of evidence of prey selection is provided by the analysis of sex ratio for the buffalo (Bovini cf. Dmanisibos), the largest ruminant of the Venta Micena assemblage. This bovid shows marked sexual dimorphism in the size of meta-carpals (Fig. 28C), thus allowing estimation of the ratio of males and females in the fossil assemblage: 26% (5/19) and 74% (14/19), respectively (i.e., approximately 1:3). These percentages are significantly different, according to a t-test (t = 9.36; p < 0.001), what suggests that predators selected female individuals, given their smaller body size.

The metapodials of the horse (E. altidens) do not show a clear bimodal pattern of size dimorphism as that exhibited by the buffalo, but linear discriminant functions developed using osteometric measurements allow to discriminate between the metapodials from males and females of Equus grevyi, the closest living analogue (both in size and shape) to the Venta Micena equid (Guererro-Alba & Palmqvist 1998). When these functions are applied to the complete metapodials of the fossil species, 26% (11/42) of them are assigned to males (9 out of 24 metacarpals and 2 out of 18 metatarsals) and 74% (31/42) to females (15 out of 24 metacarpals and 16 out of 18 metatarsals), which are proportions remarkably similar to those found in the buffalo (i.e., 1 male: 3 females).

DISCUSSION

The stratigraphic and mineralogic data presented before allow us to propound the following sedimentary interpretation of the Venta Micena stratum: generation of a mudstone under a water sheet in a lacustrine environment (margin facies); partial dessication of the palaeolake and subaerial exposure of the bottom, which preserves the previous microtopography; intense evapotranspiration and formation of an incipient calcrite paleosol (palaeoelief); development of the lowest topographic heights of ponds formed by mircrite mud, which held a small vegetational cover and experienced successive stages of dessication (rootmarks and mudcracks restricted to this zone of the stratum); and, finally, a new phase of massive generation of mudstone precipitated under water sheet conditions, that sealed the preexisiting palaeoelief. The Venta Micena assemblage, in which all size intervals for bones and species of large mammals typical in a Pleistocene palaeocommunity are represented, relies on this calcimorphic paleosol, whose irregular surface defined small trench like ponds and a surrounding area slightly more elevated, composed by a calcric duricrust which formed the surface of a lacustrine margin. The substrate of these ponds was constituted by calcareous mud, which was dessicated at least three times, and includes the majority of the fossils which were preserved in the assemblage. There is no evidence of transport by water currents, since the bones show a random pattern in their orientation, there are no rounded or polished
edges, and detritics are nearly absent from the sediment.

The surface of the bones seems to have been exposed to the effects of insolation for a very short time interval, since only 10.7% of the palaeontological sample shows incipient marks of subaerial weathering, with few shallow and small split line cracks due to insolation, and without mosaic cracking or exfoliation (weathering stage 1, Behrensmeyer 1978), what implies that the period of time...
elapsado between the death of the individuals and the definitive burial of their skeletal remains was shorter than three years. The remaining 89.5% of the bones have no evidence of subaerial exposure (weathering stage 0, 0–1 year exposed before burial). These data, as well as the absence of sedimentary infilling in the bones which were preserved complete, indicate that the bones were buried with the periosteum intact and with fat content in their microstructure (i.e., they were buried when they were still in fresh condition).

THE COLLECTING AGENCY OF BONES

The elements from the estilopod, the zeugopod, and the metapod predominate among the skeletal regions preserved, in many cases showing the original anatomical connections. The most abundant long bones are metapodials, tibiae, humeri and femori, of which only the metapodials are represented by a high percentage of complete elements. There are strong evidence which indicate that hyaenids were the biological agents responsible of the bone collecting and modifying processes, including the low number of isolated teeth and ribs, the prevalence of limb bones (of which the most abundant is the humerus in the forelimb and the tibia in the hindlimb), the high level of fragmentation of the bones (particularly proximal humeri with spiral fractures and distal tibiae with both spiral and longitudinal fractures), and the high number of gnawing marks made by premolars of large carnivores. All these features are typical of those bone assemblages collected by hyaenids (Skinner et al. 1980; Brain 1981; Horwitz & Smith 1988). Additional evidence comes from the presence of many coprolites of large carnivores associated to the bones, and from the fact that Pachy crocuta brevirostris is the only carnivore species which is represented in the Venta Micena assemblage by relatively high numbers of both juvenile and adult individuals.

The bony assemblages accumulated by hyaenids are relatively homogeneous in their composition, since they are constituted basically by limb and girdle bones (excluding phalanges), while the remaining types of bones are poorly represented, because they were not collected or due to the selective destruction in the place where the skeletal elements were accumulated. Hyaenids were responsible at Venta Micena of at least four processes: selection and transport/collection of bones; concentration; selection and alteration by the activity of adult individuals (splintering), and; selection and alteration by juvenile individuals (gnawing).

The main difference among bone assemblages collected by modern hyaenids is seen when we compare the dens of striped hyaenas (Hyaena hyaena) and those of spotted hyaenas (Crocuta crocuta). Striped hyaenas are basically scavenger carnivores due to their small size and solitary habits, which use to transport to their dens parts of the carcasses of ungulates to feed the cubs (Mills 1989); ribs and vertebrae are nearly absent from these assemblages. Spotted hyaenans are efficient hunters, due to their greater size and strong social behaviour, and do not carry regularly carrion to their dens (Ewer 1973; Mills 1989); ribs and vertebrae are slightly more abundant in their assemblages, what may owe to a lower consumption of the bones, or to denote more interest for collecting these anatomical parts. Therefore, the type of preserved assemblage depends on the spatial context where the concentration and modification of the bones took place, and also on the behavior and age class of the bone collecting agency. The former considerations are supported on the differences between the dental pattern shown by both genera of modern hyaenids, because according to Bonifay (1971) the genus Crocuta shows less differentiated cheek teeth, while the genus Hyaena presents more evolved dental features, which more closely resemble those of Pachycrocuta.

The bone assemblage preserved in Venta Micena would be generated by the selective accumulation of the skeletal remains from carcasses of ungulate prey hunted by different predators in the plains that surrounded the Pleistocene lake of Orce (predators: carnivores sensu lato; bone collecting agency: hyaenids), and by the alteration of the bones, also selective, made by both adult and juvenile hyaenids (bone modifying agency: P. brevirostris, the only eudicem carnivore in the assemblage), as it is usual in modern habitats (Sutcliffe 1970; Kruuk 1972; Brain 1981). The most abundant anatomical parts of the postcraniatal skeleton of ungulates which were preserved in the bone assemblage are the less nutritious, given their high mineral density and low fat content (for example, metapodials and distal fragments of humerus and tibia), while those bones with low structural density and high fat weight are represented by lower raw frequencies in the Venta Micena assemblage (for example, the distal epiphysis of femur, and the proximal epiphyses of both femur and tibia), because they were preferentially destroyed by hyaenans in order to extract the within bone nutrients.

All these data suggest that the activity of hyaenids took place in resting sites close to their dens. The finding of high numbers of deciduous teeth of P. brevirostris (unborn DP4 and germs of DP4) supports this hypothesis, and helps to reject the possibility that the skeletal remains were concentrated at hunting sites distant from the dens, since the youngs would not accompany adults on their
hunts, but would stay near the dens, as occurs in both modern spotted and striped hyaenas (Kruuk 1972; Mills 1989), in which juvenile individuals live in the dens until the age of 9-12 months (permanent dentition) or 12 weeks (deciduous dentition), respectively. The finding of only germs and unworn deciduous dentition implies that these teeth were not produced by tooth replacement, and it is thus a direct evidence of the death in situ of juveniles, what indicates that P. breviostris had a similar behaviour to modern *Hyaena* and not to *Crocuta*. Such conclusion is also supported by the anatomy of the P3 teeth in *Pachycrocuta*, which shows a *Hyaena* like structural pattern, opposed to that of *Crocuta*. This anatomical difference contrasts with the results of the bone modifying activity of *P. breviostris*, which are analogue to those of fossil *Crocuta* in Europe.

The distribution of teeth and bones in the Venta Micena excavation quarry shows two areas with higher density of skeletal remains, which could correspond to the bones that were dispersed at the entry of the dens; the original structure of the dens, which were excavated by adult hyaenids in dry micritic mud, was not preserved due to the effects of diagenetic compaction. The model for Venta Micena may be analogous to one of the modern dens found in Amboseli National Park (Hill 1981).

The results obtained through applying Damuth's model to the interspecific analysis of the size/abundance patterns in ungulate species from the Venta Micena assemblage indicate that the main taphonomic bias was produced by differential collecting and fragmentation by predaids of skeletal remains during an interval of time prior to their definitive burial. These biostratigraphic agents biased the composition of the palaeocommunity according to the body sizes of the species it comprised, affecting bones of smaller species more markedly. However, the structure of the original palaeocommunity was partially preserved during fossilization, and it is possible to quantitatively estimate the original representation among the unrecorded fraction. This result is congruent with what is known concerning the origin of the Venta Micena assemblage (Gilbert et al. 1992; Palmqvist et al. 1992; Mendoza et al. 1993), since all sedimentologic and taphonomic analyses indicate that bones were accumulated on a palaeosol characterized by extensive emerged zones, among which were numerous shallow ponds, places where ungulates came to drink. In this muddy environment skeletal remains of the prey of carnivores were collected by the hyaenids around the entrance of dens dug near the ponds, where they were buried rapidly as can be deduced from the low rate of subaerial weathering.

The most likely hypothesis to explain the accumulation of bones in the assemblage is that in a period of desiccation of the ponds and fall of water level, hyaenids dug small, shallow dens which would then serve almost exclusively to protect their offspring from other carnivores and from the effects of isolation; adult individuals were probably safe from other predators given their large size and social behavior. The dismembered carcasses of animals that were eaten accumulated around the entries of dens. At some time the hyaenids abandoned their dens, probably as a consequence of a slight rise of the water level of the ponds, which caused the dens, dug in dry micritic mud, to be flooded and to collapse. Immediately thereafter the water level rose considerably, precipitating the micritic limestone and sealing the entire bone assemblage.

**THE EVIDENCES FOR PREY SELECTION**

The analysis of the juvenile/adult ratios of the ungulate species identified in the assemblage in relationship to the weights estimated for adult individuals suggests different mortality age profiles depending on the size of the prey, as a consequence of selection by predators, which would increase the proportion of young and more vulnerable individuals of the species of larger body size. This interpretation agrees well with available data on prey selection by recent carnivores as a function of size and age of the ungulate prey.

The mean percentages of juvenile individuals of each African ungulate species hunted, obtained by averaging the proportions of young killed by the five main predators (wild dog, cheetah, leopard, spotted hyaena and lion), are shown in Figure 29 (Table 3, data compiled from Palmqvist et al. 1996a). Percentages were calculated only for prey species with data available on the predation of juveniles by at least three species of carnivores, except for ungulate species of larger size (>1000 kg) which are only occasionally hunted by lions and spotted hyaenas. These pooled percentages would give the figures expected in an attritional assemblage originating exclusively from the accumulation of bones of hunted animals. A highly significant direct relationship exists between the percentages of young individuals and the body weights of the ungulate species:

\[
\log(\% \text{ juveniles}) = 2.966(\pm 0.201) + 0.203(\pm 0.036) \\
\log(W); \ r = 0.805, F = 31.38 (p < 0.0001).
\]

The value for the slope in this fit (0.203) is within the 95% confidence interval of the slope that relates the percentages of juvenile individuals and the estimated weights for the ungulate species of Venta Micena (Fig. 25; slope = 0.346; standard error of slope = 0.084; confidence limits, with \( p < 0.05 = 0.156 - 0.536 \)), and reveals that the two
parameters do not differ in a statistically significant way. Therefore, the proportions of juvenile individuals representing the ungulate species in the Venta Micena assemblage truly reflect prey selection by the carnivores as a function of body size of the prey hunted.

The increase in the value of the juvenile/adult ratios in relation with the weight estimated for the ungulate species allows us to rule out the hypothesis that the fossil assemblage was formed through catastrophic mortality events that would accompany recurrent droughts; in this case the percentage of juvenile individuals of the different species would be approximately constant and size-independent. We can consequently conclude that the immense majority of the skeletal remains accumulated by hyaenas in Venta Micena came from attritional mortality in ungulate populations, caused by selective choice of carnivores.

The hypothesis of prey selection in the Venta Micena assemblage is also supported by the finding of various metapodials which show clear indications of osteopathy in the epiphysial and diaphysial regions, which would have affected the locomotive capabilities of the ungulates (Fig. 28A,B). In a study of the condition of prey, assessed from the state of the femoral marrow, Mitchell et al. (1965) found that 27% of ungulates killed by the lions, leopards, cheetahs and wild dogs were in fair or poor condition, as it may be deduced from the low quantities of fat content, while the remaining individuals preyed showed fat contents indicative of good condition. However, given the fact that the marrow test operates only at the lower end of the

<table>
<thead>
<tr>
<th>Predators</th>
<th>Prey ungulates</th>
<th>Wild dog, 25 kg (Lycaon pictus)</th>
<th>Cheetah, 50 kg (Acinonyx jubatus)</th>
<th>Leopard, 50 kg (Panthera pardus)</th>
<th>Spotted hyaena, 55 kg (Crocuta crocuta)</th>
<th>Lion, 160 kg (Panthera leo)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thomson's gazelle, 23 kg (Gazella thomsoni)</td>
<td>30%</td>
<td>38%</td>
<td>20%</td>
<td>43%</td>
<td>39%</td>
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<tr>
<td>Springbok, 31 kg (Antidorcas marsupialis)</td>
<td>--</td>
<td>22%</td>
<td>27%</td>
<td>40%</td>
<td>27%</td>
<td></td>
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<tr>
<td>Redbuck, 45 kg (Redunca arundinum)</td>
<td>65%</td>
<td>--</td>
<td>60%</td>
<td>--</td>
<td>21%</td>
<td></td>
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<tr>
<td>Impala, 51 kg (Aepyceros melampus)</td>
<td>61%</td>
<td>34%</td>
<td>28%</td>
<td>--</td>
<td>41%</td>
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<tr>
<td>Grant's gazelle, 55 kg (Gazella granti)</td>
<td>50%</td>
<td>38%</td>
<td>38%</td>
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<td>33%</td>
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<tr>
<td>Puku, 72 kg (Kobus cardowi)</td>
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<td>33%</td>
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<tr>
<td>Warthog, 75 kg (Phacochoerus aethiopicus)</td>
<td>--</td>
<td>--</td>
<td>87%</td>
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<td>46%</td>
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<tr>
<td>Hartebeest, 150 kg (Alcelaphus buselaphus)</td>
<td>64%</td>
<td>80%</td>
<td>86%</td>
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<td>33%</td>
<td>32%</td>
</tr>
<tr>
<td>Gemsbok, 150 kg (Oryx gazella)</td>
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<td>100%</td>
<td>100%</td>
<td>65%</td>
<td>35%</td>
<td></td>
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<tr>
<td>Wildebeest, 170 kg (Connochaetes taurinus)</td>
<td>83%</td>
<td>92%</td>
<td>93%</td>
<td>38%</td>
<td>27%</td>
<td></td>
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<tr>
<td>Waterbuck, 210 kg (Kobus ellipsiprymnus)</td>
<td>70%</td>
<td>100%</td>
<td>90%</td>
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<td>28%</td>
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<tr>
<td>Burchell's zebra, 230 kg (Equus burchelli)</td>
<td>28%</td>
<td>100%</td>
<td>100%</td>
<td>42%</td>
<td>37%</td>
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<tr>
<td>Eland, 560 kg (Taurotragus oryx)</td>
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<td>60%</td>
<td>16%</td>
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<tr>
<td>Buffalo, 600 kg (Syncerus caffer)</td>
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<td>--</td>
<td>100%</td>
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<td>23%</td>
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<tr>
<td>Giraffe, 1,100 kg (Giraffa camelopardalis)</td>
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<td>87%</td>
<td>71%</td>
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<tr>
<td>Black rhino, 1,200 kg (Diceros bicornis)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>90%</td>
<td>80%</td>
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</tr>
<tr>
<td>Hippo, 2,000 kg (Hippopotamus amphibius)</td>
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<td>--</td>
<td>--</td>
<td>100%</td>
<td>89%</td>
<td></td>
</tr>
<tr>
<td>White rhino, 2,500 kg (Ceratotherium simum)</td>
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<td>--</td>
<td>--</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td>Elephant, 3,800 kg (Loxodonta africana)</td>
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<td>--</td>
<td>--</td>
<td>100%</td>
<td>100%</td>
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**TABLE 3** - Mean percentages of juvenile individuals of African ungulate species hunted by the five largest African predators (data compiled from Pahnstuck et al. 1996a). **Moyennes des pourcentages des individus juvéniles d’espèces d’ongulés africains chassés par cinq grands prédateurs africains (données compilées d’après Pahnstuck et al. 1996a).**
condition scale, the proportion of unhealthly individuals preyed upon by these predators is probably underestimated. The selection of prey in poor condition is higher for those ungulate species of larger body size: 68.4% of buffalo killed by lions, in contrast with only 9.1% of hartebeest, 8.5% of wildebeest, and 23.5% of zebra (Mitchell et al. 1965; Schaller 1972). Similarly, Crisler (1956) found that the caribou the wolf catches is usually the one that slows down: at least 50% of the kills involve crippled or sick individuals, whose incidence is 1.8% or even lower in the caribou herds.

THE HUNTERS AND THEIR PREY AT VENTA MICENA

It is always difficult to determine the role played by different carnivores in a paleocommunity. Evidence that supports the model of prey selection proposed here (the results of the interspecific analysis of juvenile/adult ratios in ungulate species, the U-shaped mortality profiles, the presence of many bone diseases, and a biased intersexual ratio of large bovids) clearly indicates that most of the skeletal remains preserved in the Venta Micena assemblage come from hunted individuals. But, who were the hunters?

Four large carnivore species have been preserved in the assemblage: the great saber-tooth *Homotherium latidens*, the medium-sized saber-tooth *Megantereon whitei*, the large hyaena *Pachycrocuta brevirostris* and the wild dog *Canis (Xenocyon) falconeri*.

Saber-toothed cats, which belong to the subfamily Machairodontinae, share among others the following craniodental derived characters (see for review and references Biknevicius et al. 1996; Emerson & Radinsky 1980; Marean 1989; Van Valkenburgh & Ruff 1987):

- Elongate and flattened upper canines of two basic types: *Homotherium* (tribe Homotherine) had scimitar-shaped canines relatively short and broad, which were serrated bearing coarse crenulations, while *Megantereon* (tribe Smilodontini) showed dirk-shaped canines, extremely long, narrow, and without serrations.

- Enlarged upper incisors, which are relatively longer, thicker, more pointed and procumbent than in modern felids, and reduced, incisor-shaped lower canines. The incisor row is long and strongly curved, what suggests for saber-tooths a functional emphasis on these teeth for tearing and stripping flesh from carcasses, a task that modern felids perform with the assistance of their stout and conically shaped canines; the extremely large upper canines of the saber-tooths would probably be ineffective at the manipulation of chunks of flesh.

- Upper carnassials (P^4) with a reduced or absent protocone (lingual lobe), which is lowered away from the occlusal surface in *Megantereon*, thus removing it from its role as a hammer for bone crushing (a condition that is only present among extant felids in the hypercarnivorous cheetah), and is lost in *Homotherium*, in which there is also an anteriorly added accessory cusp. This teeth forms in saber-tooths a long thin blade, which is extremely specialized for slicing flesh, and allowed them to deflesh their prey rapidly.

- A lowered glenoid fossa, a reduced height of the coronid process, a laterally shifted angular process, and a shortened zygomatic arch. All these features allow a wider gape than that of modern felids, but suggest that the temporalis muscle was weaker. However, the temporal fossae was shorter and narrower, which indicates that the temporalis was oriented in saber-tooths more vertically and perpendicular to the tooth row than in modern felids. This increased the bite force at the carnassial (*M_2*), which was closer to the mandibular condyle, although it remained significantly lower than in felids.

- An enlarged, lowered and ventrally extended mastoid process, which is enormous relative to modern felids, what indicates that the cleido- and sterno-mastoid muscles must have been corres-
pondingly large. The occiput is in most sabertooths relatively higher and narrower than in felids, and the temporomandibular joint is located more ventrally. The mastoid process is rotated further below the skull joint so that the leverage of the neck muscle is increased, thus suggesting that a head-depressing motion was involved in the penetration of the canines.

The postcranial skeletons of scimitar-toothed and dirk-toothed machairodonts are quite different. *Homotherium* was a relatively long legged pursuit predator with the size of a modern lion, which had a comparatively large brain with an enlargedment of the optic centre, a condition similar to that of the cheetah (Rawn-Schatzinger 1992). The morphology of *Homotherium* is unique among extant and past felids, showing relative limb proportions which indicate increased cursoriality and less prey grappling capabilities than other sabertooths. The brachial index (i.e., radius length/humerus length) takes values close to or above 100%, what implies that most species of this genus preferred open habitats (Lewis 1997).

*Megantereon* was a relatively short limbed ambush hunter, with a comparatively smaller brain, showing olfactory lobes well developed. It had powerfully developed forelimbs, what suggests that a killing bite in the throat may have been coupled with the immobilization of the prey by the front limbs. Comparative multivariate analysis of postcranial measurements (Lewis 1997) indicates for *Megantereon* an overall morphology similar to that of extant jaguars, with tree catching and long distance dragging capabilities; the low value for the brachial index suggests closed habitat preferences. As it will be discussed in detail below, morphofunctional studies currently in progress of African *M. whitei* fromVenta Micena indicate that this predator generated large amounts of carrion, since it would exploit the carcasses of its prey to a small degree.

All these features indicate; that saber-toothed felids were able to hunt very large prey relative to their own size, and; that they left on the carcasses of the ungulates hunted large amounts of flesh and all within bone nutrients, which were available to be subsequently scavenged by hyaenids and hominids (Marean 1989). Sabertooths became extinct in East Africa by 1.5 Ma ago, what coincides with the emergence of the Acheulean Industrial Complex, but inhabited Eurasia until 0.5 Ma (Turner 1990, 1992). Their persistence may then explain the success of both *P. brevirostris* and hominids with Oldowan technology in Eurasia, where the Oldowan/Acheulean transition took place much later than in Africa, at approximately 0.5 Ma (i.e., when sabertooths disappeared in this continent), since the Oldowan sharp flakes were fully appropriate to scavenge on carcasses partially defleshed by saber-tooths and the cores were used by hominids in breaking bones for their marrow content.

*C. falconeri* was a hypercarnivorous canid widely distributed during the late Plioceine and early Pleistocene in the Old World (Rook 1994). This species had a large body size, comparable with that of the living northern races of *Canis lupus*, and was characterized by a relatively short neural cranium and a narrow muzzle. The sagittal crest is strong and the bullae are inflated. Features of the dentition include M3 with a relatively reduced metaconid, and M4 with a stoutly built talonid, consisting of a preeminent hypoconid relative to the entoconid, and a reduced metaconid. The lower premolars usually show accessory cusplets, and the mandibular ramus is high and heavy. The upper molars, and specially the upper carnassials, show a marked tendency to ward brachydonty; a wide occlusal basin is present at the base of the metacone and paracune in the M1, and the M2 is large. The metacarpal II has a very reduced articular facet for the metacarpal I, what indicates that the latter bone was vestigial if not absent, a condition similar to that of *Lycaon pictus*, the only extant canid with a tetradactyl forelimb (Rook 1994).

*P. brevirostris* was an African giant, short-faced hyaena relatively common in lower Pleistocene European assemblages of large mammals (Howell & Petter 1980). It had a body and skull 10-20% larger than the modern spotted hyaena, *Crocuta crocuta*, and thus probably had greater ability than the latter species for destroying carcasses and consuming bone (Turner & Antón 1996). In Europe, *P. brevirostris* is first recorded in lower Pleistocene deposits at Oliwola, and its last appearance is in the early middle Pleistocene site at Süssenborn. This species differed from other hyaenids in having a relative shortening of the distal limb segments, as reflected in the ratio of radius length to humerus length (88%; modern hyaenids range between 99% for the brown hyaena, *Parahyaena brunnea*, and 106% for the striped hyaena, *Hyaena hyaena*) and in the ratio of femur length to tibia length (74%; values of modern species range from 80% in *C. crocuta* to 89% in *H. hyaena*). These differences suggest a less cursorial life style for *P. brevirostris*, although such shortening could provide greater power and more stability to dismember and carry large pieces of carcasses obtained from aggressive scavenging (Turner & Antón 1996).

*P. brevirostris* was replaced in Europe by *Pliocrocutea perrieri* according with Turner (1992) and Turner & Antón (1996), but in Spain there is
no Pleistocene record of the latter species and P. brevirostris is substituted directly by C. crocuta. However, the finding of P. perrieri in French sites of middle Pleistocene age like Lunel Viel can be also explained by reworking of Pliocene fossils of this species, as occurs in the Spanish karstic site at Cueva Victoria. As discussed before, the extinction in Europe of P. brevirostris seems to have been linked to the decline and subsequent disappearance of machairodonts, particularly M. whitei, what implied the loss of an important source of partly-consumed carcasses, and thus a change in the interactions between flesh-eating and bone-cracking species of the carnivore guild (Martinez-Navarro & Palmqvist 1996; Turner & Antón 1996).

A possible way to deduce the respective ecological roles of the fossil carnivores preserved in the Venta Micena palaeocommunity may be to compare their hunting behavior with those of their modern analogs. Figure 30 shows the mean percentages of ungulates of different size classes (<50 kg, 50-150 kg, 150-400 kg, 400-800 kg, and >800 kg) that are killed and scavenged by the five main African predators (lion, spotted hyaena, cheetah, leopard and wild dog) (data compiled in Palmqvist et al. 1996a). As can be appreciated, lions and spotted hyaenas show similar hunting preferences according to prey body size: most kills involve animals that weigh between 50 and 150 kg. However, lions capture more ungulates of 150-400 kg, and especially more than 400 kg, while hyaenas prey more often on smaller species (<50 kg). Cheetahs and leopards show similar hunting behaviors, killing mostly ungulates of less than 50 kg. Prey of wild dogs show two peaks: ungulates of less than 50 kg, mostly Thomson’s gazelle, and animals weighing between 150 and 400 kg, like the wildebeest, which they are able to capture thanks to their cooperative hunting techniques. When these graphs are compared with that for the Venta Micena assemblage (Fig. 31), some interesting similarities emerge: the maximum for Venta Micena is in the intermediate size category (150-400 kg), similarly to the prey hunted by the lion and the wild dog, and there are two minima for the highest and lowest weight classes. The abundance in the fossil assemblage of large ungulates (>400 kg) is similar to the proportion of such prey species in lion kills. The relative scarcity of ungulates weighing less than 150 kg in comparison with the abundance of skeletal remains from species of 150-400 kg resembles the proportion of captures by wild dogs. These results suggest that two carnivores—the lion-sized saber-toothed felid H. latidens and the canid C. falconerii—played important ecological roles at Venta Micena.

However, one question remains: what was the role of the large hyaenid P. brevirostris in this palaeocommunity? Modern spotted hyaenas both kill and scavenge ungulates, depending on factors such as their interaction with lions and other predators (see Kruuk 1972). The remarkably similarity between the mean percentages of ungulates of the five size classes that are scavenged by modern spotted hyaenas (Fig. 30, data from Henschell & Skinner 1990; Kruuk 1972) and the abundance of these size categories in the fossil assemblage clearly indicates that P. brevirostris fed largely on ungulates preyed upon by other predators. The only differen-
ce between both graphs is in the abundance of small ungulates (<50 kg), which are practically absent from Venta Micena. This may be explained if we consider that these carcasses were almost entirely consumed on the spot where the large extinct hyaenas found them, rather than being carried back to their dens. A similar selective behavior has been reported among modern spotted hyaenas (Brain 1981; Kruuk 1972).

If hyaenas failed to transport the carcasses of individuals of small species to their dens, this preservation bias could then explain the scarcity of ungulate prey of very small size, which are represented in the fossil assemblage by only one distal epiphysis of a metacarpal of Caprini gen. et sp. indet. (a species weighing between 8 and 10 kg). Such selective behavior in the transport to dens of carcasses by hyaenas could then lead to poorer preservation of the young of small species in the assemblage than the juveniles of large species, thus affecting the interpretation of differential size effects on hunting success proposed here. However, this bias is only important for species of less than 50 kg, since those ungulate species weighing 50-150 kg (Hemitragus alba and Cervidae gen. et sp. indet.) are well represented in the Venta Micena collection (MNI = 14 and 20, respectively), in a proportion similar to that found among ungulates scavenged by spotted hyaenas (Fig. 30). Consequently, the increasing value of the juvenile/adult ratios as a function of body size for ungulate species weighing more than 50 kg (Fig. 25) is not an artefact of size effects on differential bone transport by hyaenas.

The results obtained clearly indicate that P. brevirostris was a bone-cracking scavenger in the Venta Micena palaeocommunity. It fed mainly on carcasses of animals killed and partially consumed by other flesh-eating carnivores, in contrast with the behaviour of modern spotted hyaenas, which are both hunters and scavengers (Kruuk 1972). The strong representation of juveniles among ungulate species identified at Venta Micena, 40.4% (80/198) of all individuals, suggests that the bone assemblage was an accumulation made by primary predators (Brain 1981; Shipman 1981; Vrba 1980). However, in primary assemblages most individuals tend to fall into a relatively restricted body size, according to the predator’s preferences, and the carnivore/ungulate ratio is usually high, while at Venta Micena the body weight distribution of ungulate species is very wide (approximately 8-6000 kg; i.e., nearly three orders of magnitude) and the value of the carnivore/ungulate ratio is rather low, only 14.1% (25/188), what indicates that the bone assemblage was predominantly a non-primary scavenged one.

These data support the previous conclusion that the Venta Micena hyaena was specialized in scavenging ungulate prey hunted selectively by other carnivores.

With respect to very large ungulate prey species identified at Venta Micena (>1000 kg), H. latidens was probably the only such carnivore species capable of hunting them, since only modern lions and spotted hyaenas can hunt juveniles or critically ill individuals of such large species. So far as other ungulates are concerned, one of the most suitable candidates for predation seems to be the canid C. falconeri, as suggested by the high frequency of osteopathologies. These canids must have pursued their prey over long distances, like modern African wild dogs, thus leading to intense selection of individuals unable to withstand prolonged running. This hypothesis is supported by the finding of numerous juveniles of ungulate species of intermediate size (46% horse, 42% large deer, and 60% buffalo), since lions and spotted hyaenas do not select young individuals among modern ungulate species of comparable sizes (Table 3) as strongly as they are represented in the Venta Micena assemblage.

The high proportion of juveniles of larger species (elephant and hippo) in the assemblage indicates that the hunting behaviour of the saber-toothed felid H. latidens was similar to that of the modern African lion. The proboscidian M. meridionalis is represented in the fossil assemblage by five individuals, four of which are juveniles. The worn molars of the remaining individual suggest that it was old and probably died of starvation, being subsequently scavenged by hyaenas. Similarly, a
study by Rwan-Schatzinger (1992) of the Fren- 
senhahn Cave assemblage, which was accumula-
ted by the great scimitar cat *Homotherium serum*, 
has revealed a very high selection (almost 100%)
of juveniles among the two proboscidean species 
identified in this site (*Mammuthus americanus* 
and *Mammuthus cf. columbi*). In contrast, other 
ugulate species of smaller body size such as 
*Mylohyus nasutus, Odocoileus virginianus* and 
*Bison* sp. are represented in this assemblage by 
much lower percentages of young individuals 
(40%, 33% and 50%, respectively). As noted above, 
lions are only able to hunt very young elephants, 
because the large size of adults makes them vir-
tually invulnerable to predation. The high selec-
tion of juveniles of large ungulate prey species in 
Venta Micena suggests then that the hunting 
behavior of large machairodonts would be similar 
to that of recent large felids, which first subdue 
prey with their claws while biting the neck, as 
opposed to specialization in the capture of large 
proboscideans by stabbing them with their elon-
gated canines and waiting for the prey to bleed to 
death, as suggested in some classic studies. 
Otherwise, the proportion of adult individuals of 
large ungulate species in the assemblage would 
have been much higher. 

With regard to the possible ecological role of *M. 
whitei* in this paleocommunity, we can offer some 
morphofunctional considerations which have been 
published elsewhere (Martínez-Navarro & 
Paläqvist 1995, 1996; Paläqvist et al. 1996a). The 
results of a comparative study of the skeletal 
remains of *M. whitei* suggest that the dimensions 
of this machairodont differ markedly depending on 
whether they are estimated from the teeth or from 
the postcranial skeleton. When body size is calcu-
lated with minimum squares regression analysis 
(Van Valkenburg 1990) of lower carnassial tooth 
(M₃) length on body weight in modern species of 
felids (i.e., the procedure followed in this work; see 
Table 1), the value obtained is of only 55 kg. This 
suggests that this African species was leopar-
dized (Martínez-Navarro & Paläqvist 1995). On 
the other hand, surface area of the diaphyseal 
cross section of the humerus in this species is 
approximately half of that in *Homotherium*, thus 
suggesting a weight of at least 100 kg for *M. 
whitei*. However, the width of the distal epiphysis of 
the humerus, which articulates with the radius, is 
greater in *M. whitei* than in a leopard or even in 
the male lion, which would suggest that the animal 
was somewhat larger than this latter species (i.e., 
around 200 kg). Obviously, these three indepen-
dent estimates differ widely, although the most 
reliable of them is probably that obtained from the 
diaphysis of the humerus, given that the section of 
this long bone bears the weight of the forepart of 
the body. If we consider this estimate correct, we 
are then dealing with a predator of about 100 kg, 
whose muscular strength used in immobilizing 
prey (estimated from the width of the distal epi-
physis of the humerus) while it used its elongated 
canines to kill was four-fold greater than would be 
suggested by its food requirements or the speed at 
which it could eat (deduced from its markedly 
reduced carnassials). We therefore have a hyper-
carnivorous felid which would presumably genera-
te large amounts of carrion, since it would exploit 
the carcasses of its prey to a small degree, thus lea-
ving enough meat and all within bone nutrients for 
the large hyaena *P. breviorostris* and for the homi-
uids. In the light of this likely situation, the recent 
discoveries of evidence on human presence both at 
Southern Spain and Georgia associated with 
African *M. whitei* (Martínez-Navarro & Paläqvist 
1995, 1996) are not surprising, since this latter 
species would have made the first dispersal of 
hominids to Eurasia in the lower Pleistocene pos-
sible, due to the greater scavenging opportunities 
it provided. 

Figure 25 shows the direct relationship between 
the abundance of juvenile individuals of those 
ugulate species preserved in the Venta Micena 
assemblage and the weight estimated for the 
adults; however, there are two distinct trends in 
this graph: the proportion of young increases gra-
dually from 14.3% in *H. alba* to 59.3% in Bovini cf. 
*Damisanisbos*, decreases to 33.3% in *Stephano-
rhinus etruscus*, and increases again from the lat-
ter species to 80.0% in *Mammuthus meridionalis*. 
According with the above discussion, the first 
group of species (< 1000 kg) were presumably hun-
ted by *M. whitei* and *C. falconeri*, while those of the 
second one (> 1000 kg) were probably predated by 
the large scimitar cat *H. latidens*. Figure 32 
shows the results of separate regression analyses in 
both groups of species. The statistical fit obtained for 
the first set of ungulates (r = 0.967, p = 0.002) is 
better than that obtained for all species in the for-
er analysis (r = 0.841, p = 0.004), which tends to 
strengthen the assumption of differences in the 
optimum prey-size for these carnivores. 

CONCLUSIONS 

- The macrovertebrate assemblage of Venta 
  Micena presents an accumulated taphonomic 
  stage and is constituted by demic and autochto-
nous palaeobiological entities recorded in situ 
  (sensu Fernández-López 1991). This bone as-
 semblage shows the highest diversity of large mam-
mals recovered from any Plio-Pleistocene lacustri-
  ne site in the Guadix-Baza basin. The density of 
bones is very high, their orientation shows a ran-
dom pattern, and more than 90% of the skeletal
elements are in contact with others. The surface of the bones was exposed to the effects of subaerial weathering for a very short time in most cases (0-1 years). The bones are not dispersed horizontally, since 20% of them are articulated and the remaining 80% are found associated. Biostratigraphic fractures, gnawing marks and coprolites are very abundant. Differential fragmentation of major long bones by hyaenas is suggested by the close relationship between the abundance of epiphyses and complete elements, and their structural density and marrow content, respectively.

- Quantitative analysis of size/abundance patterns of ungulate species at Venta Micena indicates that the preservational bias produced during the taphonomic history of this assemblage affected predominantly species of smaller body size. Once the original abundance of each species is estimated, the size/abundance relationship shows a good fit to the predictions of Damuth's model for a fossil assemblage formed by attritional mortality. The preservational characteristics of the bones from this fossil assemblage and the results of a multivariate comparison of the relative abundance of postcranial bones in assemblages from hyaena, leopard and porcupine lairs, as well as carnivore open feeding grounds and bone accumulations made by the man, suggest that the Venta Micena assemblage was formed by the accumulation of skeletal remains near the entries of shallow dens dug by hyaenas near the ponds that surrounded the Öræ lake. The use of descriptive and quantitative taphonomic analyses for the study of Venta Micena allows to propound a general model for the characterization of fossil
assemblages generated by the activity of hyaenids, for which this palaeontological site is probably an example of the collecting-modifying behaviour of Pachy crocuta breviostris.

- Interspecific analysis of the proportion of juvenile individuals among ungulates in relation to the body weights estimated for adults indicates a strong selection of prey by carnivores. This selection is corroborated by the finding of many bones with different pathologies such as arthrosis, which limited the locomotive capabilities of the animals and therefore their ability to escape predation. The sex ratio of large bovids and equids, which is highly biased in favour of females, also points to this hypothesis of prey selection, as females are more vulnerable to predation given their smaller body size. These results thus fully confirm that the Venta Micena assemblage was formed by attritional mortality produced by carnivores on the ungulate populations, and allow us to rule out that the assemblage originated from catastrophic mortality events.

- Comparison of the relative frequencies at which ungulates of different sizes are killed and scavenged by the main African predators, and the proportions in which different sized ungulates are found in the Venta Micena assemblage, suggests that hyaenids there fed largely on carcasses of animals hunted by the large mammal predator H. latidens and by the hypercarnivorous canid C. falconeri. Morphological analysis of the medium-sized sabor-tooth M. whitei shows that it may have also played a significant ecological role in this palaeocommunity as a source of ungulate carcasses for both hyaenids and hominids.

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